SHALLOW SUBTIDAL SEAWEED COMMUNITIES OF THE AGULHAS MARINE PROVINCE OF SOUTH AFRICA.

By
Deborah Wilby

Submitted in fulfillment of the requirements for the
Masters of Science in the Department of Botany,
Faculty of Science, at the
University of Cape Town.

Resubmission
January 2009

Supervisors: Prof. J.J. Bolton
Dr. R.J Anderson

Seaweed Unit
Botany Department
UCT

Science Faculty
UCT

Re: Changes undertaken for resubmission of thesis

At this stage the overall approach and design of the project could not be changed, however, many changes were made in an attempt to make the project more satisfactory, following the comments of the examiners.

The aims of the project were clarified. This project was concentrated in the shallow subtidal zone and hence the depth of sampling was relatively shallow (0-2.5m). Therefore, although investigating the impact of depth was not a primary aim of the project, the relationships it formed with biomass and species richness was still considered. Similarly, wave exposure was minimized as a factor by careful shore selection. Thus the effects of depth and wave action should not have been discussed as aims of the project, but as depth was measured (within the narrow range sampled) any effects were tested for.

At some sites 10 rather than 5 quadrats were sampled. As stated by Examiner 1, it is important to have an equal number of quadrats when looking at the species richness of different sites. Consequently, only the first five quadrats sampled at each site were used for many of the statistical analysis, including frequency of occurrence of species and the composition of the seaweed communities with regard to dominance of algal groups. Five quadrats were shown to be sufficient by use of a minimal area curve (as suggested by Examiner 1).

Wave exposure was not tested directly in this project but efforts were made to minimize the impact of this factor throughout the sampling. It would not have technically been possible to measure wave exposure at all the quadrats sampled and as such sample sites were chosen that had similar and minimal wave exposure. Other studies (Bustamante *et al* 1995, 1997, Bustamante & Branch 1996) were reviewed and the impact of wave exposure is discussed now in more depth within this project as suggested by Examiner 1.

Although it was not feasible within the study to collect adequate grazer information to properly relate grazing intensity to seaweed community structure, grazers that were sampled within the quadrats were counted to get some idea of possible grazer effects. The possible effects of grazers not measured (e.g. fish) are discussed.

Temperature data as an environmental variable in this project was gathered from a previous study (Bolton 1986). It was necessary to extrapolate from this dataset in order to get some idea of temperature regime in the sampling sites. It was not possible to measure long term temperature regime at these 11 sites. The temperature data in Bolton (1986) is the best available for the entire biogeographical region studied. In order to investigate if the mean annual temperature and temperature range are auto correlated (as suggested by Examiner 1), a correlation analysis was done between these two variables. The relationship between the two was not significant, and thus they are not auto-correlated.

General errors were rectified including grammatical and format errors (following recommendations of all examiners), as well as a standard numerical and capitalization system put in place.

Introduction

The figures, maps and tables were revised. Some were removed (i.e. the satellite images) as requested by Examiner 1, however others remained unchanged, as they are integral to the introduction of the project (Examiners 2 and 3 commended the use of maps and figures).

The articulated coralline algae section was re-written following the comments of Examiner 2.

Methods

As suggested by Examiners 1, 2 and 3 the study site descriptions were compiled into a Table thus making information more readable.

As suggested by Examiner 1 a review of figures, maps and tables was done. Additional references were also used (i.e Fricke 1979, Greenwood 1980).

A minimal area curve was added and Table summarizing the distribution in five quadrats compared with 10 quadrats as requested by Examiner 1.

Results

Biomass data changed from g/0.25m^2 to g/m^2 as recommended by Examiner 1, in order to allow comparison with other studies.

Figures and descriptive text linked more closely to increase understanding of the results, as suggested by Examiner 3.

Table 3.4 reviewed and the total biomass contributed by each species added

Discussion

Limitations of the project were addressed in more detail.

Examiner 3 makes a number of interesting points with respect to the Discussion. There have been taken into account wherever possible, within the limitations of the data obtained in this study. Also, some of them are suggestions for future studies.

General

Added missing references to the reference list and standardized the way in which references were cited.

Appendix 1 was given an appropriate title.

I hope that the changes undertaken are found to be acceptable.

Yours sincerely

Deborah Wilby

Declaration

I declare that this thesis is my own work. Where use has been made of research and information of others it has been indicated and acknowledged in the text. All work for this thesis was carried out under the supervision of Prof J.J Bolton of the Department of Botany, University of Cape Town and Dr. R.J. Anderson of the Seaweed Unit, Marine and Coastal Management.

Deborah Wilby
Department of Botany
University of Cape Town
2008

Table of contents

Acknowledgments

Firstly I would like to thank the National Research Foundation (NRF) for financial assistance for this study. There are also several people who made this thesis possible with their continued help and advice. These people include my supervisors Prof. J.J. Bolton and Dr. R.J. Anderson and also my colleague Deborah Robertson-Anderson for her assistance and patience. Thanks must also go to Chris Boothroyd, Mark Rothman and Derek Kemp of the seaweed unit for collecting some of the samples.

Finally I would like to thank my family and friends- my mother, aunt and grandmother for their continued support. To my two best friends for continually asking, "how's the project going?" and forcing me to get working. Last but not least to my husband, Levon, for his constant encouragement, understanding, love and patience; and for putting up with my repetition of species names in my sleep.

Abstract

Several aspects of seaweed ecology are poorly studied and documented in South Africa, especially the subtidal algal communities along the south coast. This study aims to investigate these communities where few other studies have been conducted. Sampling of shallow subtidal seaweed communities was undertaken at eleven sites along the south coast of South Africa from Still Bay to Mzamba. At each site a number of quadrats were placed within the shallow subtidal zone ranging in depth from 0.3m to 2.5m. Within these quadrats all algae were destructively sampled (excluding encrusting algae), invertebrate grazers present were counted, and environmental measurements were taken. These environmental measurements included depth and slope, with temperature data supplied from a previous study.

The biogeographical communities of this area were investigated using Detrended Correspondence Analysis, Canonical Correspondence Analysis and cluster analysis, in order to compare them with previous studies on the marine biogeography of the area.

In the 85 quadrats that were sampled, 97 species of Chlorophyta, Phaeophyta and Rhodophyta were found. Articulated (or geniculate) coralline red algae were very abundant in the samples, with 17 species that contributed over 44% of the biomass. There was a high number of other red algal species (54 species) but they represented only 10% of the total biomass. Green algal species were not very common (there were only 12 species) but they contributed 42% to the biomass. There were a similar number of brown algal species (14), although they only contributed 2% of the total biomass.

The westernmost sites (Still Bay and Mossel Bay), although having the lowest mean sea surface temperature, had the highest temperature range (7.4°C and 6.9°C respectively). A high range may preclude the existence of some algal species, and therefore is an important environmental factor. Silaka (roughly 10km south of Port St. Johns) has a high mean sea surface temperature (22.2°C) but a small difference between the maximum monthly mean temperature and minimum monthly mean temperature (i.e. a low range) (1.7°C).

Beach Rock (roughly 18km west of Port St. Johns) was found to have the highest average biomass and the second highest species richness. It was also found to have the highest proportion of coralline algae based on the average biomass, when compared to other red algae. Mossel Bay had the lowest biomass and Still Bay had the lowest number of species. Coralline algae were found to have the highest biomass at nine of the eleven sites, with the three most frequently occurring species being *Arthrocardia carinata* (Kützing) Johansen, *Arthrocardia corymbosa* (Lamarck) Decaisne and *Cheilosporum cultratum* subsp. *multifidum* (Kützing) Johansen.

It was hypothesised that an increase in the number of grazers and depth would both result in a decrease in biomass and species richness, and that an increase in slope would lead to an increase in biomass and number of species. It was also thought, that if there was a high temperature range at a site, then there may be a low biomass and low species diversity. However when the environmental factors were compared with biomass and number of species, a number of different relationships emerged. The only significant relationships were correlations between biomass and depth; as well as biomass correlated against the temperature range. As the depth increased the biomass decreased as hypothesised. As the temperature range increased the biomass decreased as proposed but the number of species was found not to be significantly affected by the temperature range.

Many studies have shown the importance of depth in an algal community in terms of the amount of light available for photosynthesis, but as this current study is based in a very narrow depth range in the shallow subtidal zone, it was not surprising that this relationship was not important. However it was found that there was a positive correlation between depth and the number of grazers, although this could be related to an inter-relationship between depth and wave action in shallow waters (not measured).

Presence/absence data was analysed using Detrended Correspondence Analysis (DECORANA). The presence/absence data placed western sites and eastern sites along a biogeographical gradient. Other separation in this plot divided the three sites in the extreme east from one another i.e. Mzamba from Silaka and Beach Rock, and this could be attributed to the fairly large difference in sea surface temperatures between these three sites and the different species unique to these sites. The DECORANA for the biomass data separated Still Bay on the one side of the plot and Haga Haga and Glen Muir on the other.

This could be attributed to the difference in temperature range between these sample sites, with Still Bay having a high temperature range (7.4°C) and the latter two sites having a relatively low temperature range (2.9°C and 2.8°C respectively).

Various environmental variables affect algal communities differently. In order to assess which of these variables come into play at which of the study sites, several Canonical Correspondence Analysis (CANOCO) were undertaken using both biomass and presence/absence data. It was found that the temperature range separates samples from Beach Rock, Silaka and Mzamba; and that both the minimum and maximum monthly temperatures separated samples from Still Bay and Mossel Bay.

Cluster analysis of the presence/absence data from the eleven sites suggested that the most easterly sites were distinct from those further west, with a break occurring in the Beach Rock area (just west of Port St. Johns), as also shown in the DECORANA plots. The cluster analysis for the biomass data shows many different groupings due to the high variability between the biomass at the different sample sites. Looking at biogeographical analysis of historical presence/absence data from a previous study, there appears to be a break, or change in algal composition, in the Port Alfred area, which is slightly further east than where the break was found with presence/absence data in the shallow subtidal community samples in the current study.

Further study needs to be conducted in this shallow subtidal zone in the Agulhas Marine Province and eastern overlap area with greater focus on the possible environmental factors that influence community structure. Studies regarding nutrient levels, sand inundation and grazing impact need to be undertaken. This project goes some way to describing these diverse shallow subtidal communities by providing a list of which species dominate in this area and which environmental factors appear important in shaping these algal communities. The current study also shows that the floristic communities around the south coast of South Africa undergo several changes in their composition and structure and that not only maximum temperature, but also annual temperature ranges influence the biogeography of these communities. There are significant biogeographical breaks in at least one area suggesting that future measures must be undertaken to protect all of these unique environments.

Chapter 1: Introduction

Coastal areas are often regarded as the interface between three habitats, namely the land, air and sea (Boaden & Seed 1985). These regions vary from rocky outcrops and shores to sandy beaches and estuaries, each with their own unique environmental conditions and community structures. They are important areas both environmentally, in offering a diverse range of habitats to a wide range of species; and economically, in providing numerous food sources and significant ecotourism opportunities. However coastal habitats are in a state of almost constant change and thus render rocky shores one of the most stressful habitats for both animals and plants (Branch & Branch 1981). Coastal areas are one of the most dynamic and diverse environments, yet they are still one of the least well studied environments and as such there is a need for further research of these regions, especially of the subtidal zone.

Rocky shores are perhaps the best researched of all coastal habitats, with copious amounts of literature available for the intertidal and, to a lesser extent, the subtidal regions (Branch & Branch 1981, Boaden & Seed 1985, Field & Griffiths 1991, Littler & Kitching 1996, Knox 2000). Much work has been undertaken regarding intertidal species of both fauna and flora, whilst these organisms are often understudied in the subtidal regions (Wood 1987, Anderson & Stegenga 1989, Leliaert *et al.* 2000). This is mainly due to the difficulty of working under water with the strong wave action often experienced, and the necessary use of scuba gear or submersibles (Lobban & Harrison 1994). From the small amount of data available it is thought that the shallow subtidal zone (0-30m) has more seaweed species and greater macroalgal biomass than any other marine habitat (Foster *et al.* 1985).

Ecological studies of seaweed in South Africa began in the 1930's with the main focus on vertical zonation and biogeography within the intertidal region (Stegenga *et al.* 1997). Only in the 1970's did study of the subtidal zone in South Africa begin, often with great difficulty and as such there is a lack of comprehensive data and literature for this region (Anderson & Stegenga 1989, Stegenga *et al.* 1997). The south coast region of South Africa is especially poorly documented (Anderson & Stegenga 1989, Bolton & Anderson 1997, Bolton & Stegenga 2002). There is, for example, only one published study of subtidal algal communities for the entire south coast and that is limited to Bird Island near Port Elizabeth

(Anderson & Stegenga 1989). It is therefore necessary that future work be undertaken to document the community structure and composition of subtidal zones, not only in South Africa, but also in other regions of the world where there are important yet understudied rocky shore environments.

Rocky shore environments

Rocky shores are harsh environments to inhabit, with daily exposure to the air (in the intertidal zone) and variable wave action (in the shallow subtidal and intertidal zones) (Branch & Branch 1981). Thus organisms living in these zones need to be adapted to the different conditions experienced at different levels on the shore, leading to vertical zonation of a rocky shore (Branch & Branch 1981, Boaden & Seed 1985). While desiccation is one of the main effects determining the community structure of the intertidal zone, this factor is not important in the subtidal zone. Zonation patterns in this lower zone are largely determined by light, water movement and biotic factors (Brown & Jarman 1978, Branch & Branch 1981, Boaden & Seed 1985, South & Whittick 1987, Wood 1987, Lüning 1990, Lobban & Harrison 1994, Bustamante *et al.* 1995, 1997, Bustamante & Branch 1996, Stegenga *et al.* 1997, Lubke 1998, Leliaert *et al.* 2000).

One of the most obvious components of a rocky shore community is the macroalgae (the other being attached animals) (Littler & Kitching 1996). Seaweeds are major primary producers in both the intertidal and the shallow subtidal regions and are therefore an important source of food and shelter for marine animals (Branch & Branch 1981, Littler & Kitching 1996, Knox 2000). Algae not only affect the lives of the marine organisms on rocky shores by influencing shore ecology, but they also affect human lives (Littler & Kitching 1996). People have used seaweed for thousands of years and roughly 500 species are used globally for the production of food, fertiliser and chemical products (Stegenga *et al.* 1997, Anderson *et al.* 2003).

Biogeography

Knowledge of the distribution and abundance of marine flora and fauna is essential for an understanding of both the origins of characteristic biotas as well as the effects of climate change (Bolton *et al.* 2001).

Distribution of marine species worldwide is governed by a number of environmental and biological factors (Brown & Jarman 1978, Wood 1987). These include

1) Sea water temperature (Brown & Jarman 1978, Bolton 1986, 1996, Bolton & Stegenga 1987, Breeman 1988, Lüning 1990, Bolton & Anderson 1997, Leliaert *et al.* 2000, Bolton & Stegenga 2002, Bolton *et al.* 2004). It was suggested that warm temperate regions tend to have very rich floras (900-1100 species); while rich (600-700 species) and poor floras (300-400 species) are spread throughout temperate and tropical regions; and very low diversity (roughly 200 species) is found in polar regions (Bolton 1994). Bolton & Anderson (1990) concluded that "not only the absolute ranges of seaweed, but also the structure and composition of seaweed on a biogeographical scale can be correlated with seawater temperature regime."

2) Substratum type- this can be either hard (i.e. rocks) or soft (sand) which strongly affects the biota of an area (Wood 1987). However this applies mainly to animals as almost all seaweeds only grow on hard substrata, except in very sheltered conditions (De Clerck *et al.* 2005).

3) Light and depth- this is of special importance in subtidal areas where the amount of light affects the depth to which algae can survive (South & Whittick 1987, Wood 1987, Lüning 1990, Lubke 1998). Algae can only survive in the photic zone where light is sufficient for photosynthesis. However some species can grow deeper than others e.g. some crustose red algae can survive at lower light intensities than other types of seaweed (South & Whittick 1987, Wood 1987, Lüning 1990, Lubke 1998, De Clerck *et al.* 2005). Littler *et al.* (1986) have recorded the deepest macroalgal life- crustose coralline red algae found at 268m near the Bahamas.

4) Water movement in the form of tidal currents and wave action (Wood 1987). Wave action influences the physical nature of a coastline by creating and modifying habitats, thus impacting the marine biota of an area (Lubke 1998). The movement of water caused by the tide is one of the most important factors in distribution of fauna and flora as it affects the zonation of the shore (Lubke 1998). Local variation in community composition is strongly linked to wave action especially in intertidal zones of southern Africa (Bustamante & Branch 1996, Bustamante *et al.* 1997). The two studies found

that on wave exposed shores around the coast of South Africa, there was a higher community biomass but a lower number of species than on sheltered shores.

5) Salinity and water quality- poor quality water (e.g. high levels of turbidity) can lead to increased stress for marine organisms (Wood 1987). High levels of turbidity increase the light attenuation ability of the water thus reducing the depth at which algae can grow. Salinity or the amount of dissolved inorganic substances in the water column also has an important impact on marine systems (Boaden & Seed 1985).

6) Sand inundation affects the water quality and light penetration of a body of water. Sand and sediment are major agents of disturbance associated with water movement and are especially detrimental to algal spores (Lobban & Harrison 1994). Spores may settle on sediment only to be washed away, or they may be shadowed or smothered when sediment settles on them (Lobban & Harrison 1994).

7) Herbivory has a relatively localised effect on algae growth and community composition in both temperate and tropical communities (Hay & Fenical 1988). Korpinen *et al.* (2007) found that grazing reduces algal colonisation at the community level but there was little effect on the diversity of algae. Grazing promotes the growth of certain types of algae (Anderson *et al.* 2005) and to persist the environment algae must either escape, deter or tolerate herbivory (Hay & Fenical 1988).

Spalding *et al.* (2007) divide the world's coastal and shelf areas into12 different marine provinces, each then separated into a number of ecoregions and realms. The classifications were based on "taxonomic configurations, influenced by evolutionary history, patterns of dispersal, and isolation" (Spalding *et al.* 2007). These provinces are:

1) Arctic (one ecoregion)
2) Temperate Northern Atlantic (six ecoregions)
3) Temperate Northern Pacific (four ecoregions)
4) Tropical Atlantic (six ecoregions)
5) Western Indo-Pacific (seven ecoregions)
6) Central Indo-Pacific (12 ecoregions)
7) Eastern Indo-Pacific (six ecoregions)
8) Tropical Eastern Pacific (two ecoregions)

9) Temperate South America (five ecoregions)

10) Temperate Southern Africa (three ecoregions)

11) Temperate Australasia (six ecoregions)

12) Southern Ocean (four ecoregions)

The area for this study falls within Temperate Southern Africa, in the Agulhas and Natal Regions.

Various authors discuss the hypothesis that species diversity of an area (and thus biogeographical patterns of seaweed distribution) could be linked to historical events in geological time and the current environmental conditions of an area (Hoek 1984, Hommersand 1986, Lüning 1990, Bolton 1994, Bustamante *et al.* 1995, 1997, Bustamante & Branch 1996). Bolton (1996) suggested that high diversity may be due to a coastline experiencing the same, or similar, conditions for a long period of geological time and relatively small variations between the winter and summer sea water temperatures. Santelices *et al.* (in press) discuss the idea that global seaweed species richness is related on a logarithimic scale to the length of the coastline. These studies go some way to identifying and classifying the biogeographical distribution of seaweeds for some rocky shores but much work is still necessary. An in-depth comprehension of biogeographical boundaries is needed to be able to investigate the potential effects of global climate change and also to assist in the development of ecologically representative systems of protected areas (Bolton *et al.* 2001, Spalding *et al.* 2007).

<u>South African seaweed biogeography</u>

With a coastline extending almost 3000km from the Orange River mouth (the border with Namibia) to Ponto de Ouro (the border with Mozambique), South Africa has many diverse coastal regions (Stegenga & Bolton 1992, Critchley *et al.* 1998). Many of these regions (especially the subtidal zones) have not been studied in any great detail resulting in an incomplete understanding of the country's diverse marine fauna and flora. Much is known about the south west of the South African coast between Saldanha Bay and Still Bay, but moving further east, detailed studies are rare. Very little information is known or available of the south and east coast subtidal zones (Bolton & Anderson, 1997).

South Africa has an extremely diverse seaweed flora (roughly 900 species) with a high level of endemism in most regions (Bustamante *et al.* 1997, Bolton 1999, Leliaert *et al.* 2001, Bolton & Stegenga 2002, Bolton *et al.* 2004). This high level of diversity is mainly due to the wide range of conditions along the coastline of the country, resulting from a cool current (Benguela) on the west coast and a warm current (Agulhas) on the east coast (Lubke 1988). These factors create variable conditions around the coast providing a range of marine climatic regions.

Two current systems, namely the Agulhas Current and the Benguela Current, dominate the coastal waters around South Africa and interact in the extreme south of the region (Brown & Jarman 1978, Field & Griffiths 1991, Bustamante & Branch 1996) (Figure 1.1).

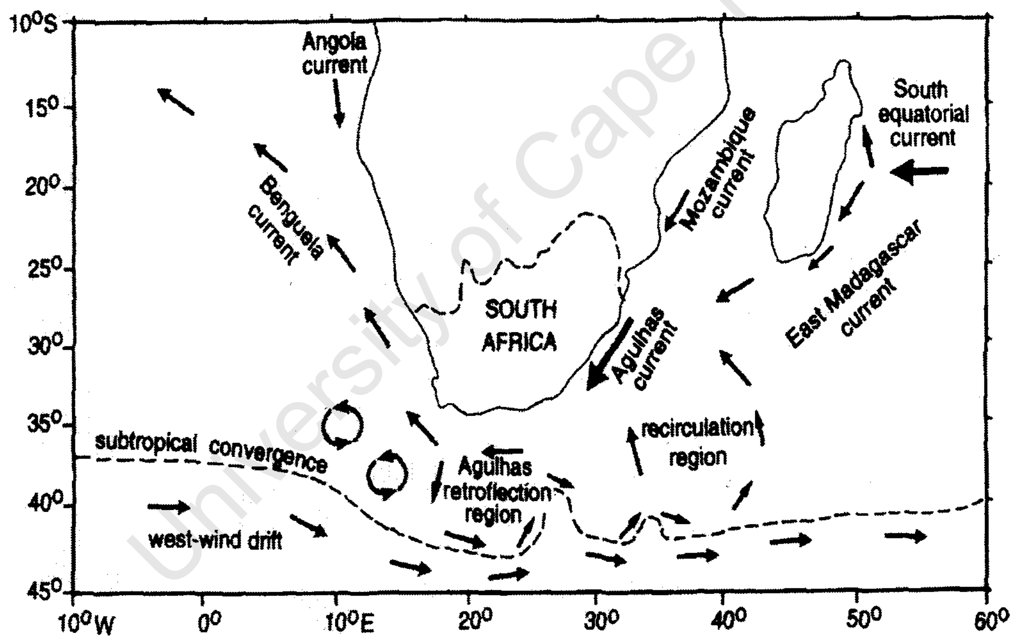

Figure 1.1: Map showing the flow of the ocean currents around the coast of southern Africa (Walker 1989).

The Benguela Current is a northward, slow flowing current on the west coast of southern Africa from Cape Agulhas to southern Angola (Brown & Jarman 1978, Field & Griffiths 1991, Bustamante & Branch 1996, Critchley *et al.* 1998). The water originates at the Sub-tropical Convergence, from Atlantic central water and is therefore colder than that on the east and south coast of the country (Brown & Jarman 1978, Farrell *et al.* 1993, Critchley *et al.* 1998). In this area along the coast there are also variable upwelling events that bring even colder water to the surface (between 8°C to 14°C) (Field & Griffiths 1991). This upwelling leads to a high biomass on intertidal shores but a low number of species (Bustamante *et al.* 1995, Bustamante & Branch 1996).

The tropical Agulhas Current flows from Mozambique down the east coast of South Africa bringing warm water from the Indian Ocean (Brown & Jarman 1978, Ross 1988, Bustamante & Branch 1996, Critchley *et al.* 1998). It is a fast flowing, warm western boundary current with the average surface water temperature between 21°C and 27°C (Ross 1988, Field & Griffiths 1991, Critchley *et al.* 1998). It flows southwards along the continental shelf break to the vicinity of Cape St. Lucia from where it diverges (just before the Agulhas Bank) from the coast and moves back towards the east (Brown & Jarman 1978, Heydorn *et al.* 1978, De Clerck *et al.* 2005). The warm water and southward flow of the Agulhas Current facilitates the spread of tropical marine organisms to the south coast of South Africa (Brown & Jarman 1978, Farrell *et al.* 1993, Critchley *et al.* 1998).

These two currents, with their different characteristics, meet, mix and interact over the Agulhas Bank- a broad continental shelf stretching 250km offshore along the south coast of South Africa, from Port Elizabeth to Cape Agulhas (Brown & Jarman 1978, Largier & Swart 1987, Ross 1988, Field & Griffiths 1991). This fluctuation between cold and warm sea currents results in a number of "diverse regions and a whole variety of habitats along the Eastern Cape coast…providing a wide range of ecological niches" (Lubke 1988).

The hydrography of the inshore waters between the coastline and the Agulhas Current is complex and little is known of it (Ross 1988, Field & Griffiths 1991). In this region between the coast and the Agulhas Current there is a colder counter current that moves eastwards (Ross 1988). The conditions in this area are very variable with sea surface temperature ranging from 15°C to 20°C, and with cold upwelling in summer in certain areas often bringing the temperature down considerably (Zoutendyk 1973, Brown & Jarman 1978). This region experiences very localised and brief cells of dynamic upwelling, as well as easterly winds blowing over several prominent south coast capes which increase the effect of the localised upwelling (Bustamante *et al.* 1995).

Stephenson (1948) divided the South African coastline into three coastal regions based on ecological studies he carried out in the intertidal zone (also discussed in Brown & Jarman 1978, Bolton 1986, Seagrief 1988, Bolton & Stegenga 1987, 1990, 2002, Bustamante & Branch 1996, Bolton & Anderson 1997, Critchley *et al.* 1998, Lubke & Seagrief 1998). The zones are:

1) the cold temperate west coast province – Port Nolloth to Kommetjie
2) the warm temperate south coast province – Cape Agulhas to Port Edward
3) the subtropical east coast province – Port Edward to Umpangazi

Stephenson (1948) also recognized two regions of overlap viz:

1) the western overlap – Kommetjie to Cape Agulhas
2) the eastern overlap – Port Elizabeth to Port Edward

With just a few later amendments and addition of information these three marine provinces have in the past been widely accepted (Bolton 1986, Bolton & Stegenga 1987, Critchley *et al.* 1988, Jackelman *et al.* 1991, Farrell *et al.* 1993, 1994, Bustamante & Branch 1996,). Bolton (1986) considered the flora of the west coast to be cool temperate rather than cold temperate as described by Stephenson (1948) but still distinct from the warm temperate south coast flora. Other modifications are discussed in Field & Griffiths (1991), Emanuel *et al.* (1992), Stegenga & Bolton (1992), Bolton & Anderson (1997), Critchley *et al.* (1998). However these biogeographical divisions devised for the coastline of South Africa are primarily based on intertidal species and the community structure in this zone. Little is known of subtidal communities, thus there is a lack of data on which to base any subtidal biogeographical distribution.

Bolton & Anderson (1997) and Bolton (1999) describe South Africa's marine provinces on the basis of seaweed distribution in both the intertidal and subtidal zone. They suggest that the country has, for the most part, temperate seawater conditions with two temperate marine provinces: the cool temperate Benguela Marine Province (Stephenson's cold temperate west coast province) and the warm temperate Agulhas Marine Province (Stephenson's warm temperate south coast province) (Lüning 1990, Bolton & Anderson 1997). They also identify a third area namely the Indo-West Pacific province from the KwaZulu-Natal north coast to Mozambique (the northern part of Stephenson's subtropical east coast province). According to these authors there are also two regions of overlap, one between the Benguela province and the Agulhas province, namely the Western overlap (Stephenson's western overlap); and one between the Agulhas province and the Indo-West Pacific province, namely the Eastern overlap (Stephenson's eastern overlap and the southern part of the subtropical east coast province). Figure 1.2 shows clearly where one zone starts and another begins, with the areas of overlap in-between the Benguela and Agulhas province.

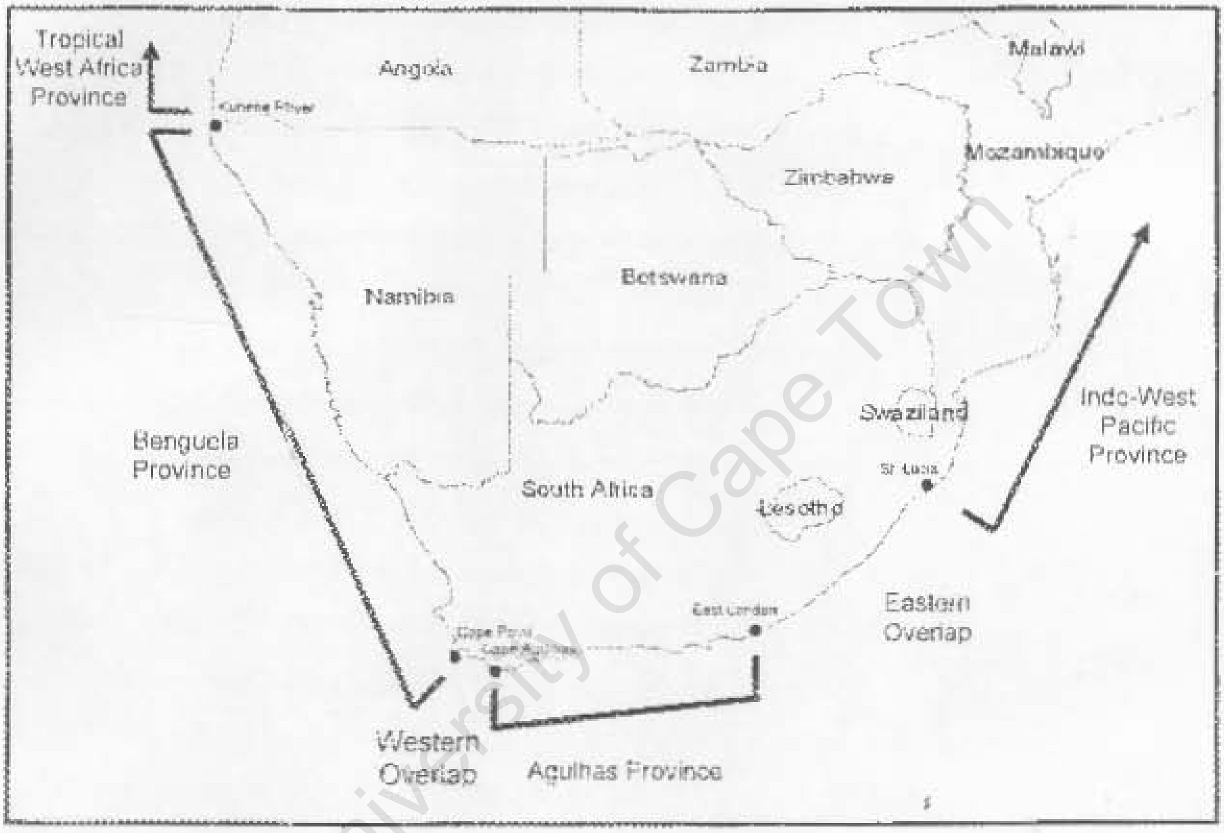

Figure 1.2: Map showing the different marine phytogeographic provinces around South Africa (Bolton & Anderson 1997, Bolton *et al.* 2004).

The Benguela Marine Province is found along the west coast of South Africa and the whole of the Namibian coast, and has a greater diversity of species in the more southerly region (Bolton & Anderson 1997). It is influenced by upwelling from the Benguela Current, with inshore temperatures often decreasing to 8°C for short periods (Shannon 1985, Bolton 1986, Bolton & Anderson 1997). The Benguela Marine Province is characterised by large Laminarian kelps in the subtidal zone and is best described as "cool temperate" (Bolton & Anderson 1997), as monthly mean seawater temperatures are never below 10°C. Minimum monthly means below 10 °C have been used as a criterion for a 'cold temperate' designation (Lüning, 1990).

The Agulhas Marine Province is along the south coast of South Africa. There is a much lower occurrence of cool-water upwelling in this area making the sea surface temperature generally higher than experienced in the Benguela Marine Province (Bolton & Anderson 1997). Within the Agulhas Marine Province (between Cape Agulhas and East London) the mean annual sea surface temperature ranges between 17°C and 18°C (discussed later) (Bolton & Anderson 1997).

The Agulhas Marine Province

South Africa has nine geographical (political) provinces, four of which have a border with the sea. The Agulhas Marine Province stretches from Cape Agulhas (in the Western Cape) to a region between Algoa Bay and Port St Johns (in the Eastern Cape) (Brown & Jarman 1978). This marine province stretches along the south and lower east coast, roughly 660km (Lubke 1998) and falls within Stephenson's warm temperate south coast province and eastern overlap area. Several authors differ in their opinion of the locality of the eastern border of this province so in order to help to identify the accurate position of the border of this province this study includes samples up to the KwaZulu-Natal border.

In the Eastern Cape, from the Kei River mouth to Cape St. Francis, there are wide sandy beaches with a few rocky headlands and from Morgan Bay to Double Mouth there are predominantly cliffs (Seagrief 1988). The Eastern Cape coastline is very exposed and subject to strong winds and seas, which in turn affects the community dynamics and composition of a rocky shore environment (Lubke1988, Seagrief 1988). The seaweed flora of the northern east coast (KZN) is closely related to the tropical Indian Ocean seaweed floras (Lüning 1990, Bolton *et al.* 2004). Previous studies show that the Eastern Cape flora has primary affinities with the subtropical flora of the Indian Ocean (KZN) with components related to species from south and west Australia and Japan, but also with numerous species in common with the west coast (Brown & Jarman 1978, Hommersand 1986).

Along the southern coast shoreline, rocky cliffs are more common and there are long stretches of coastline without sandy beaches (i.e. between Knysna and Robberg near Plettenberg Bay) (Lubke 1998). The temperature along the south coast can vary considerably as shown in Table 3.6.

Seawater temperature is the most important factor controlling the geographical distribution of seaweeds (Brown & Jarman 1978, Breeman 1988, Lüning 1990). On the south coast of South Africa, the lowest temperature in an area may limit the distribution of subtropical species, while the highest temperature may deter colonisation by cool water (west coast) species (Brown & Jarman 1978, Lüning 1990). Similarly, typical south coast species will be adapted to water temperatures in this region.

The seaweed biota of the south coast experiences intermittent pulses of cold water and lacks the tropical components found in the warmer water north of Durban such as reef forming corals (Brown & Jarman 1978, Lubke & Seagrief 1998). The deepwater reds that are predominant in subtidal zones on the west coast are absent (Brown & Jarman 1978, Lubke & Seagrief 1998, Lüning 1990). These canopy algae are replaced to an extent by *Sargassum heterophyllum* and *Anthophycus longifolius* (Lüning 1990). Other dominant species include *Caulerpa filiformis, C. holmesiana, Hypnea spicifera, Plocamium corallorhiza, Dictyota dichotoma* and *Halimeda cuneata* (Brown & Jarman 1978).

The south coast is considered to have the highest levels of seaweed diversity among seaweed floras on the South African coast (Bustamante & Branch 1996, Bolton & Stegenga 2002). There are high levels of endemism with regard to red algal species although the endemic species tend to "drop out" when moving in a north-easterly direction around the coast and are replaced by more widespread Indo-Pacific tropical elements (Hommersand 1986). Despite the south coast having the highest seaweed diversity in South Africa, the composition of algal communities has been little studied (Bolton & Stegenga 1990, 2002).

The marine flora of the Agulhas Marine Province is especially poorly documented from a floristic and ecological perspective, with only a few studies having been undertaken in this region (Stephenson *et al.* 1937, Seagrief 1967, Bolton & Stegenga 1987). When it comes to subtidal seaweed community studies in this marine province, the only information available is that from Anderson & Stegenga (1989). They looked at subtidal algal communities at

Bird Island in the central south coast and found three distinct communities that were apparently related to the amount of water movement or wave exposure in the area. The exposed sites were dominated by *Gelidium pteridifolium* (at depths down to ca. 9 to 10m) and the less exposed sites dominated by *Plocamium corallorhiza, P. rigidum and Pachychaeta brachyarthra* (at depths of ca. 5m). The deep water communities (at 22m) were considered to experience the least water movement and were dominated by *Peysonnelia capensis* and various articulated corallines.

Bolton & Anderson (1997) proposed that the findings, regarding water movement, from Anderson & Stegenga (1989) can be extended to other similar habitats along the south coast of South Africa. In many subtidal areas of the south coast (i.e. in shallow reefs and gullies) articulated coralline species, such as *Amphiroa ephedaea*; *Arthrocardia duthiae* and *Corallina officinalis* predominate (Bolton & Anderson 1997). Other species are also abundant in the south coast subtidal zone, including some foliose algae such as species of *Plocamium*, *Caulerpa*, *Laurencia*, *Codium* and *Dictyota* (Bolton & Anderson 1997). In the shallow subtidal areas of the Agulhas province, algal community diversity is heavily influenced by herbivory compared to the Benguela province and for this reason, many of the seaweed species may contain herbivore- deterrent chemicals (Bolton & Anderson 1997). Articulated coralline algae are well defended against grazing by certain herbivores (Johansen 1981, Bold & Wynne 1985, Anderson & Stegenga 1989, Bolton & Anderson 1997). As previously mentioned, they were found to be relatively abundant by Anderson & Stegenga (1989) and other studies have found them important in many shallow subtidal communities (Bustamante & Branch 1996). (Johansen 1977, Brown & Jarman 1978, Branch & Branch 1981, Boaden & Seed 1985, Bolton & Stegenga 1987, Bolton & Anderson 1997).

<u>Articulated coralline Red Algae</u>

Coralline algae are present in most rocky shore ecosystems both intertidally and subtidally and are important components of marine benthic communities (Johansen 1977, 1981, Bold & Wynne 1985, Woelkerling 1988, Bustamante & Branch 1996). They compete successfully with other marine organisms especially in the upper subtidal zone, often by forming associations with other animals and plants (Johansen 1981).

Crustose corallines are not dealt with or identified within this study due to difficulties in sampling and identification. Articulated (= non-geniculate) corallines are abundant on the east and south coast of South Africa (Johansen 1977, Bustamante & Branch 1996), but seldom so on the west coast except in the overlap zone between Cape Point and Cape Agulhas.

Summary and aims

Along the south coast of South Africa (as defined here from Cape Agulhas to the southern KZN border) the shallow subtidal zone is characterised by low-growing species of predominately red and green algae with a large number of coralline species (Brown & Jarman 1978). This south coast area, for the purpose of this study, includes the biogeographical south coast, plus the eastern overlap region of Stephenson (1948). The western overlap was not included, as the shallow subtidal communities are clearly different, being dominated by inshore kelp beds (*Ecklonia maxima*) (Stegenga *et al.* 1997). Kelp beds are qualitatively different to the communities in the study area, which lack large kelps.

In some areas of South Africa relatively little is still known about the floral (and faunal) communities that inhabit subtidal environments. Whilst ecological studies of intertidal seaweed began in the 1930's looking at vertical zonation and biogeography; studies of the shallow subtidal region began only in the 1970's and purely on a taxonomic basis (Stegenga *et al.* 1997). Much of the seaweed research in South Africa up until recently was focused on the west coast and east (KZN) coast and both the intertidal and subtidal zones of the south have been poorly studied (Field & Griffiths 1991, Bolton & Anderson 1997, Critchley *et al.* 1998, De Clerk *et al.*2005). Thus there is a particular need for research to be conducted in the shallow subtidal region of the entire south coast (reportedly one of the most highly diverse regions of the whole coast) (Stegenga & Bolton 1992, Bolton & Stegenga 2002).

Bolton (1999) suggests that the main priority for further work in South Africa needs to include detailed investigations of the flora of the overlap area with tropical East Africa and more specifically the south coast. Bolton & Stegenga (2002) also suggest that detailed systematic and biogeographical investigations on the overlap between seaweeds of the temperate south coast and those of the tropical Indian Ocean are needed with particular attention to subtidal collections and vegetation descriptions.

This study aims to focus on the shallow subtidal seaweed community of the south coast as this is thought to be a very productive zone. The main hypotheses that are tested in this study, are:

1) Sea water temperature is a major driver of seaweed species presence and absence, and it is hypothesised that temperature regime will correlate not only with species presence/absence but also community composition as these two components (species presence/absence and community composition) are invariably linked.

2) An increase in biomass will result in a decrease in species richness. A large amount of one or two large species will "crowd" an area and leave very little space for smaller species. Therefore areas with high biomass will have few species.

Other factors will affect species occurrence, abundance and dominance, such as slope of sampled substratum, depth, wave action and grazer abundance. The study is confined to a narrow depth range to minimise depth effects. Also, sites were chosen with similar wave action characteristics. The effects of slope and grazer abundance within the quadrat were investigated.

This study also aims to determine the biogeographical affinities of species assemblages in these shallow subtidal communities. The results from the biogeographical data will be compared to current ideas on the biogeographic patterns of inshore benthic organisms on this coast, such as Stephenson (1944, 1948), Bolton & Anderson (1997). This would facilitate future studies into the changing biogeographical regions of South Africa thus providing insight into any future major environmental changes especially concerning varying sea temperatures.

Chapter 2: Methods

The focus of this study was on the broader south coast of South Africa from Mzamba (near the northern border of the Eastern Cape) to Still Bay, approximately 161km from Cape Agulhas. Sites were selected for study along the coastline based on the geology of the area (i.e. if it was a rocky shore) and the accessibility of the location. There were eleven sites in total which were spaced along the coast in order to sample different regions of this ecologically diverse area and all are exposed to moderate wave action. These sites were selected so to minimise the variation of wave exposure between the sites and as such were all exposed to moderate wave action. The samples, although placed randomly at the sample sites, were in the same locality in order to minimise variation in many different environmental factors (i.e. sand inundation, wave exposure, temperature differences).

Some sample sites were located close to one another (i.e. Beach Rock and Silaka were roughly 11km apart) due to the ease of sampling, however the average distance between the sites was 104km. At each site either five or ten samples (50 x 50cm quadrat collections of seaweed) were collected depending on the sea conditions and ability to dive on that day. At some of the sample sites it was logistically difficult to collect ten samples. Therefore a minimal area curve (fig 2.1) was created to investigate whether five quadrats were adequate to fully represent the diversity of the area.

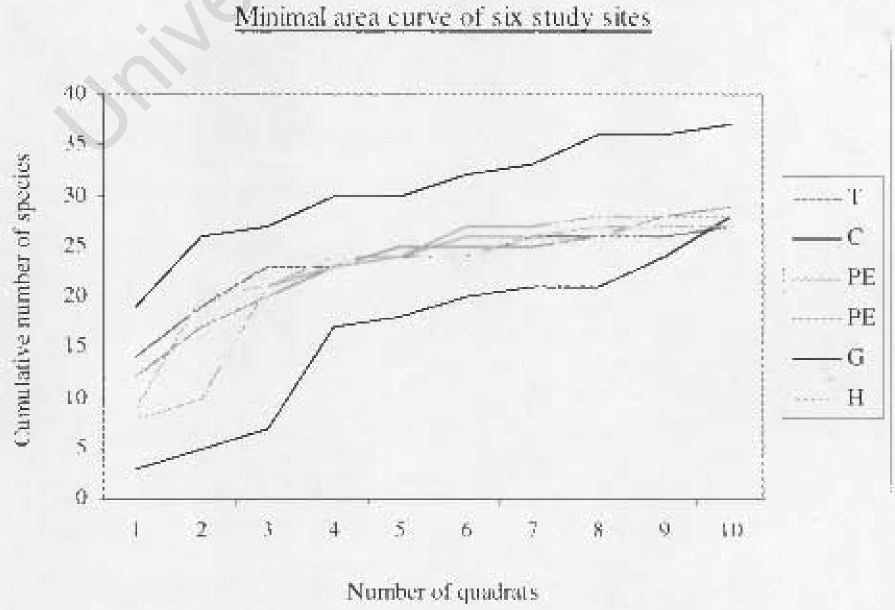

Figure 2.1: Minimal area curve for the six sample sites where ten quadrats were collected.

The percentage of total species that occured in the five quadrats at these six sites are also shown in Table 2.1

Table 2.1: The number of species found at the six asmple sites, with the average percentage of species found in five quadrats.

Sample site	**Number of species in five quadrats**	**Number of total species (ten quadrats)**	**Percentage (of total species found in five quadrats)**
Tstsikamma	24	27	89
Cape St. Francis	18	28	64
Port Elizabeth	24	27	89
Port Alfred	25	29	86
Glen Muir	30	37	81
Haga Haga	24	28	86
Total average percentage			82.5

Figure 2.1 and Table 2.1 clearly show that five quadrats is a reasonable number of quadrats to sample as on average more than 80% of the species in ten quadrats at each site were found in the first five quadrats. Where possible, it would be advantagous to sample ten quadrats, however this was not always possible during this study.

Each site was given an abbreviation, usually a number and the first letter of it's name, seen in brackets below (Fig 2.1). The distance from Cape Agulhas to each site (along the coast) was also measured, using Google Earth®, for use in data analysis. Sampling took place over a year (March 2005 to March 2006) within the shallow subtidal zone as described below.

Sampling

Sampling was done within the shallow subtidal zone (0-2.5m below MLWS) during the spring low tides, using either snorkel or SCUBA. At each site five 50x50cm ($0.25cm^2$) quadrats were placed in a more-or-less straight line from just below the low water mark to either a maximum depth of 2.5m, or where the rock ended in sand, or where wave action prevented further access. Quadrats were spaced approximately equally along this "visual transect" but topographical anomalies (e.g. deep crevices) and completely seaweed free surfaces (an urchin covered "bare rock", sand filled holes in gulleys) were avoided. One diver was able to sample five quadrats within the one and a half to two hours available over a low tide. When more divers were available, or when the site could be revisited the following day, a second set of five quadrats were sampled.

In each of the quadrats a range of data was collected including physical and biological information. These included both the depth of the quadrat, and the degree of slope that each quadrat was placed on ranging from flat (0^o) to vertical (90^o). Also the number of grazers present was recorded with the larger and more mobile ones noted visually and counted in *situ* (i.e. limpets and adult urchins) whilst smaller ones (juvenile urchins and limpets) were collected with the seaweed and the presence of any fish was noted. This was done for logistical reasons, and in order to minimise the disturbance and impact this study had on the marine community.

In *situ* identification of the seaweed was impossible, so all seaweeds within each quadrat were scraped off the rocks and placed in a 5% formalin in seawater solution. The seaweed was later identified at the University of Cape Town with the use of reference books and pressed specimens from the Bolus Herbarium. Once identified and weighed (wet weight), seaweed species were either pressed, preserved in formalin, or semi-permanent microscope slides were made for later comparisions between different samples and study sites.

Study sites

Sampling was done at eleven sites and at a number of different depths at each site. The depths are all measured relative to the mean low water spring tide. Positions of the sites are shown in Figure 2.2 and discussed briefly later (Table 2.2).

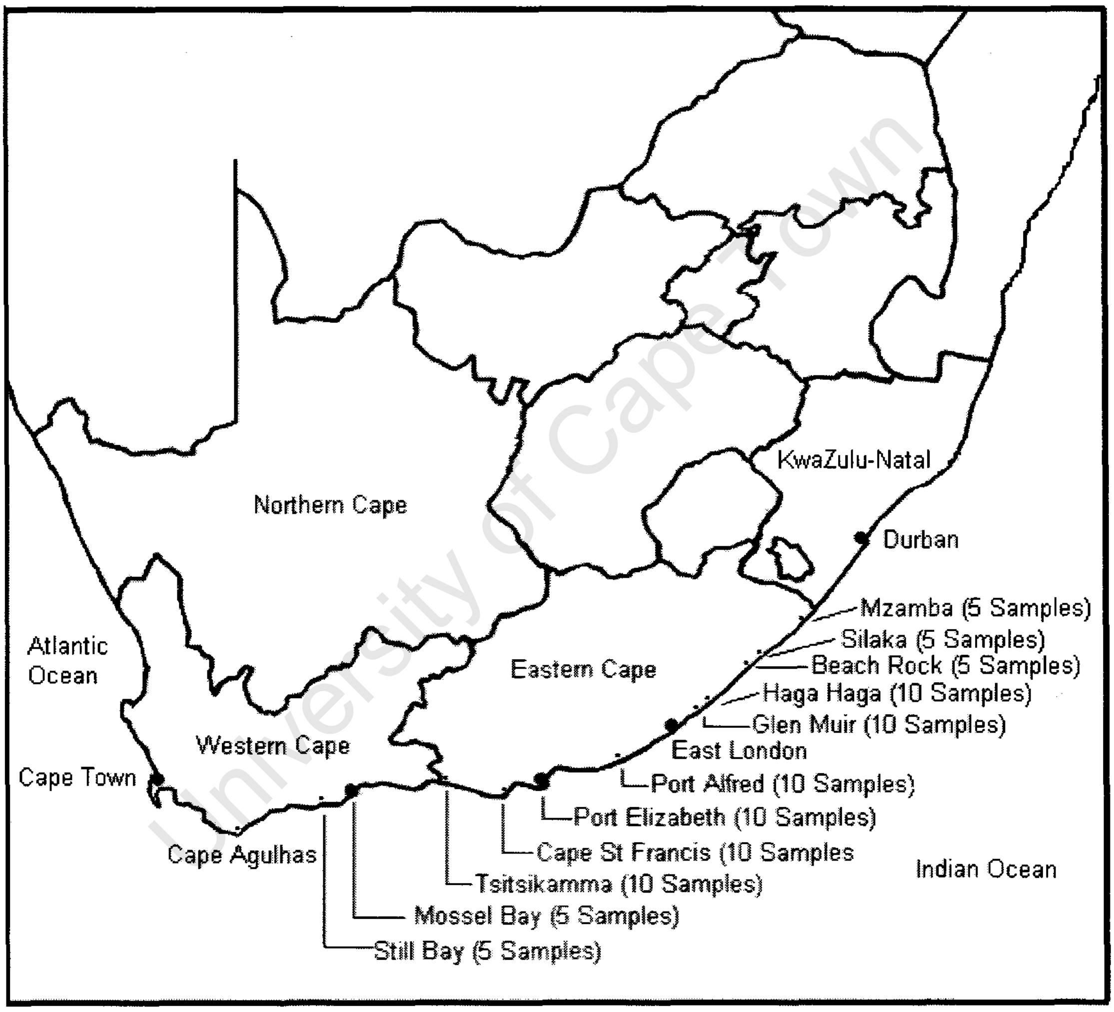

Figure 2.2: Map showing the eleven study sites with the number of samples collected. East London is marked as a point of reference only, no sampling was done here.

Sample Site	Abbreviation	Coordinates	Distance from Cape Agulhas (km)	Date Sampled	Number of quadrats	Depth Range (m)	Brief description
Still Bay (Morris Point)	1ST	34°23'30"S 21°25'40"E	161	30/03/2006	5	0.3-1.5	This area was to some extent protected at low tide by submerged reef in front of site.
Mossel Bay (Haaibanke)	2MB	34°00'10" S 22°00'07"E	245	30/01/2006	5	0.5-1.5	Generally calm but presence of Pyura indicates good water movement. Protected from westerly winds and swells but exposed to easterlies.
Tstsikamma border	3T	34°00'45" S 23°29'30"E	395	31/01/2006	10	0.5-2.1	Situated between Platbank and Grootbank. First five quadrats were exposed to swell with lots of water movement, latter five quadrats were sheltered from intense wave action, although both sites were exposed to waves at high tide.
Cape St. Francis (Seal Point)	4C	34°12'45"S 24°49'50"E	527	20/05/2005	10	1.3-2.5	Fairly exposed to swell. Rocky area with only small sandy beach in the near proximity thus very little sand in the seaweed community.
Port Elizabeth (Shoenmakerskop and Willow Glen)	5PE	34° 02'30"S 25° 32'50"E and 34°02'45"S 25°36'30"E	611	15/10/2005	10	0.5-2.5	Two sites were sampled, each with five quadrats, but they were extremely close to each other. Both were exposed to prevailing westerly swells.

Port Alfred (Shark Bay)	6P	33°36'45"S 26°53'30"E	772	11/07/2005	10	1.1-1.5	Protected at low tide by sand banks and therefore a fairly large amount of sand was present. However the area was underlain by a gently sloping rock shelf.
Glen Muir	7G	32°52'50"S 28°06'00"E	912	18/10/2005	10	0.5-1.1	Mostly rocky outcrops and rocky gulleys with a sandy beach behind the rocks.
Haga Haga	8H	32°45'54"S 28°15'06"E	935	17/10/2005	10	0.5-2.1	Rocky shelves and gulleys with sand banks in front providing protection at low tide. Small beach in close proximity resulting in sand being found in many quadrats.
Beach Rock	9B	31°21'00"S 29°26'30"E	1096	11/03/2005	5	0.5-1.6	Site was just south of Port St. John, and wave exposed. Sampling conducted in gulley open to the sea that was protected at low tide by shallow sand banks in front of it.
Silaka	10S	31°39'30"S 29°30'30"E	1108	9/03/2005	5	0.5-1.4	Close to Port St. John in an area that was sheltered at low tide but exposed to waves at high tide. Sampling done in bottom of a gulley (slope 0^{o}) and on the sides (slope ca. 60^{o})
Mzamba	11MZ	31°06'S 30°11'E	1203	21/08/2005	5	1	Fairly flat shelves of rock extending some distance from the shore. Exposed to wave action but protected at low tide by a shallow shelf.

Temperature data

Sea surface temperatures were not measured at the site during sampling as this would have only provided data for one day. Instead data from Bolton (1986) was used in order to gain information regarding mean annual temperature as well as temperature range (see Figure 2.3). A previous study of South Africa (Bustamante *et al.* 1997) also used temperature data for analysis, however rock temperature data (using thermcouples attached to rock surfaces) was collected over a three day period and not the sea surface temperature. McQuaid and Branch (1984) when studying an area of South African rocky shore coastline for influence of sea temperature, substratum and wave exposure, classified the sites merely as warm or cold. The data used in this present study is more comprehensive than most data used in previous similar studies, having been measured over a nine year period by the South African Maritime Weather Office.

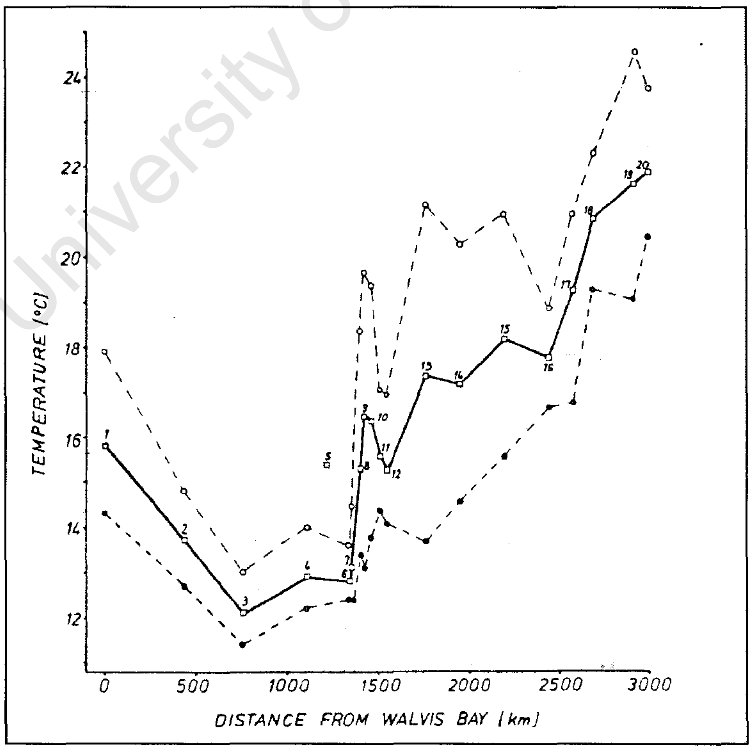

Figure 2.3: Graph of sea surface temperature accumulated from the Maritime Weather Office. The solid line is the mean annual temperature, the top dotted line is the highest monthly mean temperture and the lower dotted line being the lowest monthly mean temperature (Bolton 1986). Point 13 is Still Bay, 15 Port Elizabeth, and 17 Port St. Johns (near to Silaka)

The x-axis of this graph represents the distance from Walvis Bay (km) but in the current study all distances were calculated from Cape Agulhas. Only four of the sites in the current study have detailed temperature measurements in the dataset of Bolton (1986): 13 (Still Bay), 15 (Port Elizabeth), 16 (East London) and 17 (Port St. Johns). Data for other sites was estimated by interpolation (see Table 3.6). These temperature values were then used in ecological analysis, to test whether the biomass and number of species are affected by this variable. The mean annual temperature for each sample site was plotted against the temperature range in order to determine if there was a correlation between these two variables.

Analysis

Data was used for two different types of analysis. Firstly, for ecological analysis in order to describe the composition and diversity of the subtidal algal communities in the Agulhas Marine Province. Secondly, for biogeographical analysis, to compare the algal communities and structure found along this south coast with existing biogeographical classifications of this area.

Ecology

Data from the sampling was compiled into Excel spreadsheets including biomass, presence/absence and environmental data. From this, the total biomass for each species, each site and each algal group (Rhodophyta, Phaeophyta and Chlorophyta) was calculated, as well as the average biomass per quadrat at each site (i.e. the total site biomass divided by the number of quadrats sampled) ($g/0.25m^2$). This biomass was multiplied by four in order to obtain data in g/m^2. In this way, data from this study could be more easily compared to data from other studies.

Graphs were drawn (using Excel) of the total and average biomass. For many of the other analyses (frequency of occurrence table, table of the most abundant species, species diversity graphs), an equal number of 5 quadrats from each site were used. From the species area curve and table 2.1 it is clear that five quadrats are a good representation of the species present, and thus for each sample site the information from the first five quadrats only was used.

A table was created of the 20 species that occur most often and are most abundant in terms of biomass. This again used information from just the first five quadrats at each sample site. The frequency of occurrence for all the species (not just those found in the top 20 tables) was plotted against the biomass of the species to determine if there was any relationship between these two variables.

The distance from Cape Agulhas to each of the sites was measured (in km) using Google Earth and this was then used to interpolate the temperature data for those sites which were not measured in the dataset of Bolton (1986). Figure 2.2 plots the distance from Walvis Bay (x-axis) against the sea surface temperature (y-axis), This distance axis was used in conjunction with the measurement of the distance between Walvis Bay and Cape Agulhas, and from Cape Agulhas to the eleven study sites. Temperature readings were then interpolated from the graph to give information regarding the sea surface temperature patterns around the south coast.

The environmental data collected at the site (i.e. depth, slope and the number of grazers) as well as the temperature data, were all plotted against both biomass and number of species in correlation analyses using Statistica Ver. 6.0. These environmental analyses were done to investigate any possible relationships between environmental and biological patterns. Each graph has a r- and p- value attached in order to draw conclusions regarding the significance of these relationships. The r-value, also called the correlation coefficient, measures the strength and direction of a linear relationship between variables. The p-value measures the probability that two variables are significantly correlated.

Although the relationship between depth and biomass, and depth and number of species, did not form part of the main aims (or hypothesis) of the project, these variables were tested in correlation analysis to see if they had any significant effect. Depth range in this study was limited as sampling was undertaken in the shallow subtidal zone, and as such it was thought to be an inconsequential environmental variable. However it was analysed to rule out any impact or influence it may have on the seaweed communities.

The benthic grazers that were included in the analysis were sea urchins (class Echinoidea) larger than 1cm, winkles (class Gastropoda, subclass Prosobranchia), limpets (class Gastropoda, subclass Prosobranchia), chitons (class Polyplacophora) and sea hares (class

Gastropoda, subclass Heterobranchia). Little information is available regarding the feeding of urchins and at what size they begin to feed on macroalgae. De Riddler & Lawrence (1982) state that juvenile urchins differ in their feeding habitats depending on species, but that *Strongylocentrotus intermedius* smaller than 1cm are detritus feeders rather than grazers. Most of the urchins in this study were *Parchinus angulosus,* that feed on a wide diet of algae but most especially on kelp (Anderson *pers. com.*, Fricke 1979, Greenwood 1980). For this study only urchins larger than 1cm were included in the analysis as it was assumed that those smaller than this would have little impact on the mature seaweed community. The number of grazers in each quadrat was also plotted against the depth of the sample to test for any relationship between the number of grazers and depth and therefore to provide further insight into the effect of increasing depth on the seaweed communities.

The number of seaweed species was correlated against the biomass of the seaweed in each quadrat, to test if there was a relationship between the biomass and species diversity.

<u>Biogeography</u>

In order to investigate biogeographical distribution patterns, three types of multivariate analysis were undertaken, namely DECORANA, CANOCO and agglomerate cluster analysis.

The main aim of cluster analysis is to find the natural groupings of objects that may form a complete population (Chatfield & Collins 1980). Individuals (i.e. samples) that are similar to one another are grouped together while individuals in another group are dissimilar from this first group (Chatfield & Collins 1980). This method therefore measures the similarity or dissimilarity of a population (Chatfield & Collins 1980). The Jaccard index was used as the measure of similarity for the presence/absence data and the Euclidean distance used for the biomass data. Quantitative data or biomass data is most commonly assessed using Euclidean distance as the measurement and the Jaccard index is best used when assessing presence/absence data.

Detrended correspondence analysis (DECORANA) is used to analyse the species data independently of environmental factors. It is presented as a plot in which each point represents a quadrat and where the distance between them reflects the similarity or dissimilarity between the quadrats (Begon *et al.* 1996). Four DECORANA plots were created using Community Analysis Package Ver. 4.0 (Pisces Conservation Ltd.), two using biomass data (one for the samples and one for the species) and two for presence/absence data (one for the samples and one for the species) with no down weighting for rare species in any of the plots.

Canonical Correspondence Analysis (CANOCO) was run using both the biological and environmental data to produce a plot where the axis scores are constrained by environmental variables (Kent & Coker 1992, Evans 2005). This analysis was done using ECOM Ver. 1.3 (Pisces Conservation Ltd.) and illustrates which of the environmental factors are responsible for the differences between the algal communities. The environmental variables that were tested included slope, number of grazers, depth and temperature data, and were correlated firstly using biomass data and then the presence/absence data.

Agglomerative cluster analysis is a hierarchical clustering method used to illustrate relationships between samples, which creates a dendogram or hierarchical tree. Two dendrograms were created using Community Analysis Package Ver. 4.0 (Pisces Conservation Ltd.) via agglomerative cluster analysis, using average linkage and choosing Jaccard as the similarity measurement. One of the hierarchical trees used biomass data and the other used presence/absence data.

The Jaccard index measures similarity between samples and is calculated as follows:
Jaccard equation: a / (a+b+c)
where a is the number if species present in both samples

b is the number of species present in sample one but missing from sample two and

c is the number of species missing in sample one but present in sample two

(Pisces 2007).

Bolton & Stegenga (2002) undertook a study of the entire coastline of South Africa in order to investigate the species diversity of the different coastal regions. They split the coastline into contiguous 50km sections and then compiled a species lists for each section based on previously recorded information. The species presence/absence lists used in Bolton & Stegenga (2002) have been updated (Bolton & Anderson unpublished) and an analysis of the data for the south coast is used and compared with the shallow subtidal data. The Bolton & Anderson unpublished data includes all records from the literature and local collections of seaweed present in the 50km sections. The results accumulated during the sampling for this study were compared to those from Bolton & Stegenga (2002). This was mainly done to ascertain whether the biogeographical breaks found along the coastline in the two studies were in similar regions.

Chapter 3: Results

In total 85 quadrats were sampled, with 97 species being found, 11 of which could not be identified to species level although they were recognised as distinct taxa. This data is summarised in Table 3.1 below. Within the total area covered by the quadrats the mean algal wet weight was found to be 2.33kg/m^2. There were only 12 species of Chlorophyta in the whole sample but they contributed 42.82% to the total biomass. Articulated corallines showed a similar pattern- with only 17 species but contributing 44.69% to the total biomass. The other red algal species (Rhodophyta) totalled 54 species but contributed only 10.42% to the biomass suggesting that the species that were found were generally small. Phaeophyta contributed 14 species to the total number of species and only just over 2% of the biomass, signifying that those found were small and only found in small quantities and at few sites. All species found across the whole study site are listed in Table 3.2, which also shows the sites at which the seaweed species were found.

Table 3.1: Biomass and species richness across all 85 quadrats illustrating the distribution within the three algal groups.

Algal group	Number of species	% of number of species	% of the total biomass
Chlorophyta	12	12.37	42.82
Phaeophyta	14	14.43	2.07
Rhodophyta – Corallines	17	17.53	44.69
– other reds	54	55.67	10.42
Total	97	100%	100%

Table 3.2: Seaweed species list with the species number used in the biological analysis and the occurrence of each species. The group corresponds to which group of algae they belong i.e. R=red; G=green; B=brown; AC=articulated coralline. The sample site abbreviations used here are the same as described in the Methods but without the number due to formatting constraints.

Species name	Species no.	Group	ST	MB	T	C	PE	P	G	H	B	S	MZ
Acrosorium acrospermum	1	R				x		x			x	x	x
Acrosorium maculatum	2	R							x	x			
Amphiroa anceps	3	AC	x	x	x	x	x	x	x				
Amphiroa beauvoisii	4	AC	x	x	x	x			x	x		x	
Amphiroa bowerbankii	5	AC							x		x	x	x
Amphiroa ephedraea	6	AC		x	x	x	x	x	x	x	x	x	
Anotrichium tenue	7	R							x				
Apoglossum spathulatum	8	R		x	x				x	x			
Arthrocardia carinata	9	AC			x	x	x	x	x	x	x	x	x
Arthrocardia corymbosa	10	AC	x	x	x	x		x	x	x	x	x	x
Arthrocardia flabellata	11	AC			x	x	x	x	x	x			
Botryocladia madagascariensis	12	R									x	x	
Calliblepharis fimbriata	13	R					x						
Callithamnion cordatum	14	R	x	x									
Carpoblepharis sp.	15	R									x		
Carpomitra longicarpa	16	B											x
Caulerpa bartoniae	17	G								x			
Caulerpa filiformis	18	G	x					x	x	x	x	x	
Caulerpa holmesiana	19	G				x	x		x	x			
Caulerpa zeyheri	20	G								x		x	
Ceramiae indet dw1	21	R			x						x		
Ceramium camouii	22	R		x									
Ceramium sp1	23	R						x	x				
Ceramium sp2	24	R	x	x									
Chaetomorpha spiralis	25	G							x				x
Champia compressa	26	R			x	x	x			x	x	x	x
Cheilosporum cultratum subsp. multifidum	27	AC	x	x	x	x	x	x	x	x	x	x	

Cheilosporum proliferum	28	G									x	x	
Cheilosporum sagittatum	29	G		x	x	x	x	x	x	x	x		
Codium lucasii	30	G	x		x		x						
Codium lucasii subsp. capense	31	G	x								x		
Codium stephensiae	32	G			x			x					
Colpomenia sinuosa	33	B	x	x									
Corallina officinalis	34	AC		x	x	x	x	x	x	x			
Corallina sp1	35	AC										x	
Corallina sp2	36	AC						x					
Dasya scoparia	37	R							x				
Derbesia sp.	38	G							x				
Dichotomaria diessingiana	39	R						x					
Dictyomenia stephensonii	40	R									x		x
Dictyopteris ligulata	41	B	x	x								x	
Dictyota dichotoma	42	B	x	x	x	x		x					
Dictyota dichotoma var. intricata	43	B										x	
Dictyota liturata	44	B							x				
Erythroglossum sp.	45	R				x							
Exallosorus harveyanus	46	B							x				
Falkenbergia rufolanosa	47	R		x									
Gelidium abbottiorum	48	R						x			x		
Gelidium pteridifolium	49	R			x						x		x
Gelidium reptans	50	R		x									
Gracilaria beckeri	51	R						x					
Griffithsia confervoides	52	R				x			x	x			
Halimeda cuneata	53	G					x	x	x	x	x	x	x
Haliptilon subulatum	54	AC	x		x	x	x	x	x	x		x	x
Heterosiphonia dubia	55	R									x		
Hypnea rosea	56	R			x		x	x	x			x	x
Hypnea tenuis	57	R		x					x	x			x
Inkyuleea beckeri	58	R											x
Jania adhaerens	59	AC					x		x				x
Jania crassa	60	AC						x	x				x
Jania intermedia	61	AC				x		x	x	x	x	x	x
Laurencia complanata	62	R									x	x	

Laurencia flexuosa	63	R	x	x	x		x			x	x	x	
Laurencia glomerata	64	R	x		x	x	x	x				x	
Laurencia natalensis	65	R		x		x	x			x			
Laurencia obtusa	66	R	x	x	x			x					
Martensia elegans	67	R											x
Metamastophora flabellata	68	R									x		x
Nienburgia serrata	69	R					x			x			
Peyssonnelia capensis	70	R									x		
Peyssonnelia replicata	71	R				x							
Platysiphonia miniata	72	R					x						
Plocamium beckeri	73	R					x		x		x	x	
Plocamium corallorhiza	74	R		x	x	x	x	x	x				x
Plocamium rigidum	75	R			x	x	x						
Plocamium suhrii	76	R	x	x	x	x	x	x		x			x
Polysiphonia incompta	77	R	x	x	x								
Polysiphonia sp. indet.	78	R		x									
Portieria hornemannii	79	R	x	x			x				x		
Portieria tripinnata	80	R			x								
Pseudocodium de-vriesii	81	G							x		x		
Pterosiphonia cloiophylla	82	R		x							x	x	
Pterosiphonia stangeri	83	R				x							
Rhodymeniaceae sp.	84	R									x		
Rhodymenia natalensis	85	R				x			x	x	x	x	
Rhodymenia sp.	86	R							x				
Sarcodia dentata	87	R						x					
Sargassum heterophyllum	88	B				x	x			x			
Sphacelaria brachygona	89	B	x	x	x								
Spyridia cupressina	90	R					x	x	x	x	x		
Spyridia horridula	91	R									x	x	
Stypocaulon funiculare	92	B							x				
Stypopodium multipartitum	93	B	x										x
Stypopodium zonale	94	B									x		
Valonia macrophysa	95	G										x	
Zonaria harveyana	96	B				x							x
Zonaria subarticulata	97	B	x			x		x	x	x	x		

The average biomass for each site (g/m^2) (Figure 3.1) generally increased from west to east, peaking at Glen Muir and Beach Rock (the latter having the highest average biomass). There is also a general increase in the biomass of red algal species moving from west to east, excluding Glen Muir and Haga Haga where there were high levels of green biomass. Brown algae contributed very little to the biomass of all the sites.

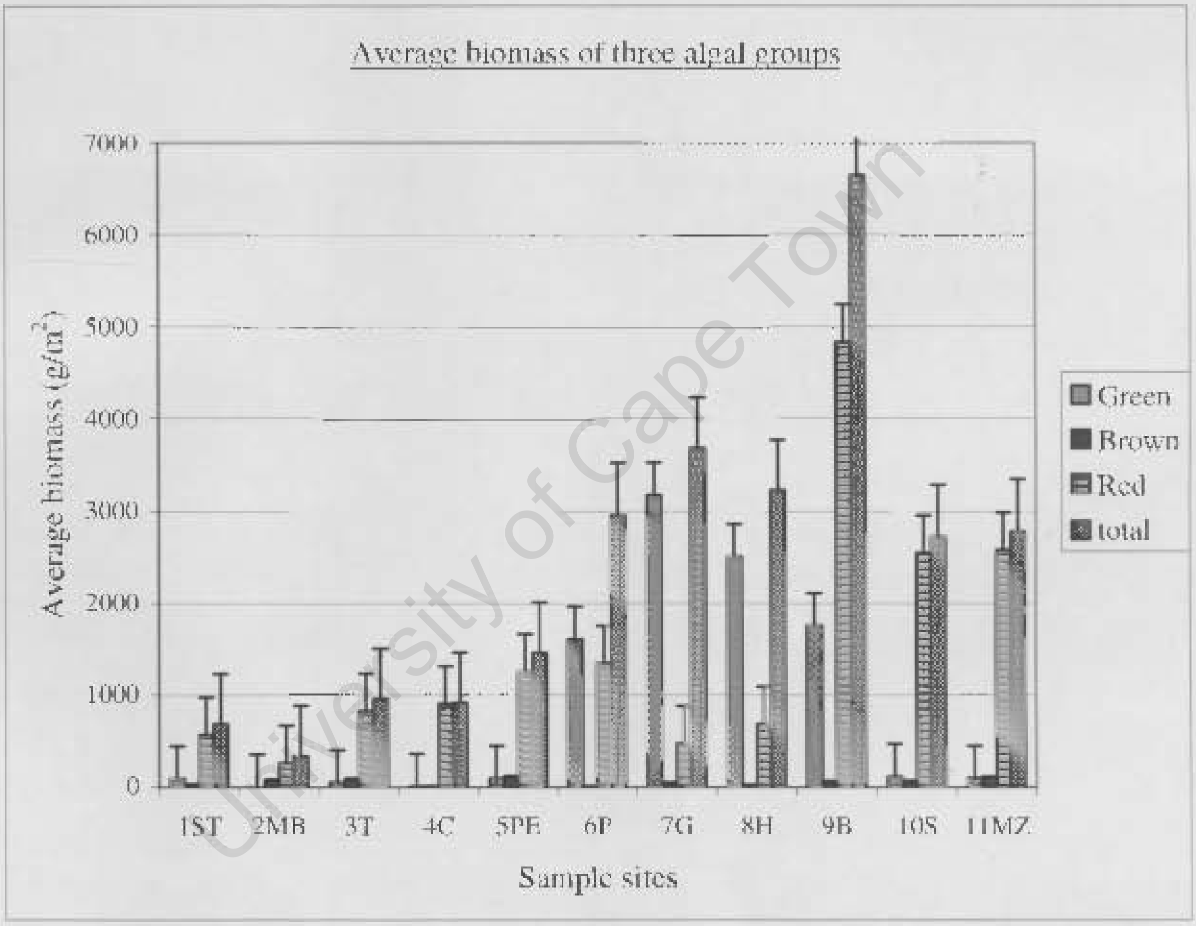

Figure 3.1: The average biomass (wet weight) of red, green and brown seaweed species and total average biomass across all the study sites with standard error bars.

When the biomass of the red algae was separated into articulated coralline algae and other red species, corallines were clearly shown to contribute the most to the biomass (Figure 3.2). The three easternmost sites have very much higher coralline biomass than the other eight sites. Nevertheless, red algal biomass is dominated by corallines at all sites except the two westernmost sites.

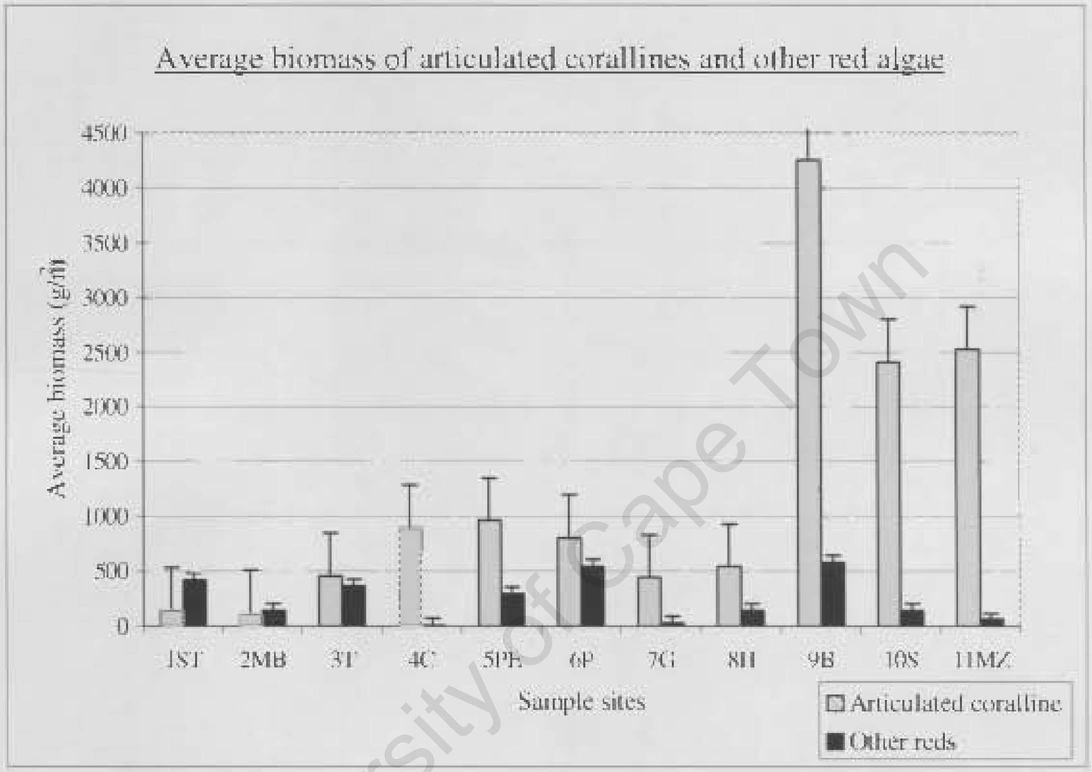

Figure 3.2: The average biomass (wet weight) of articulated coralline algae and other red seaweed species for each study site with standard error bars.

The total range of number of species across the sites was 17 to 34 species, with six out of the eleven sites having 25 to 30 species. The total number of species present was highest at Beach Rock, Glen Muir and Silaka, but there was little difference between the 11 sites (see Figure 3.3). Green and brown algal species together contributed roughly one quarter of the total number of species at each site, with red algae contributing the remaining three quarters of species. The species richness remained relatively stable or unchanged across the eleven sites, with Cape St. Francis having the lowest number of species and the third lowest average biomass.

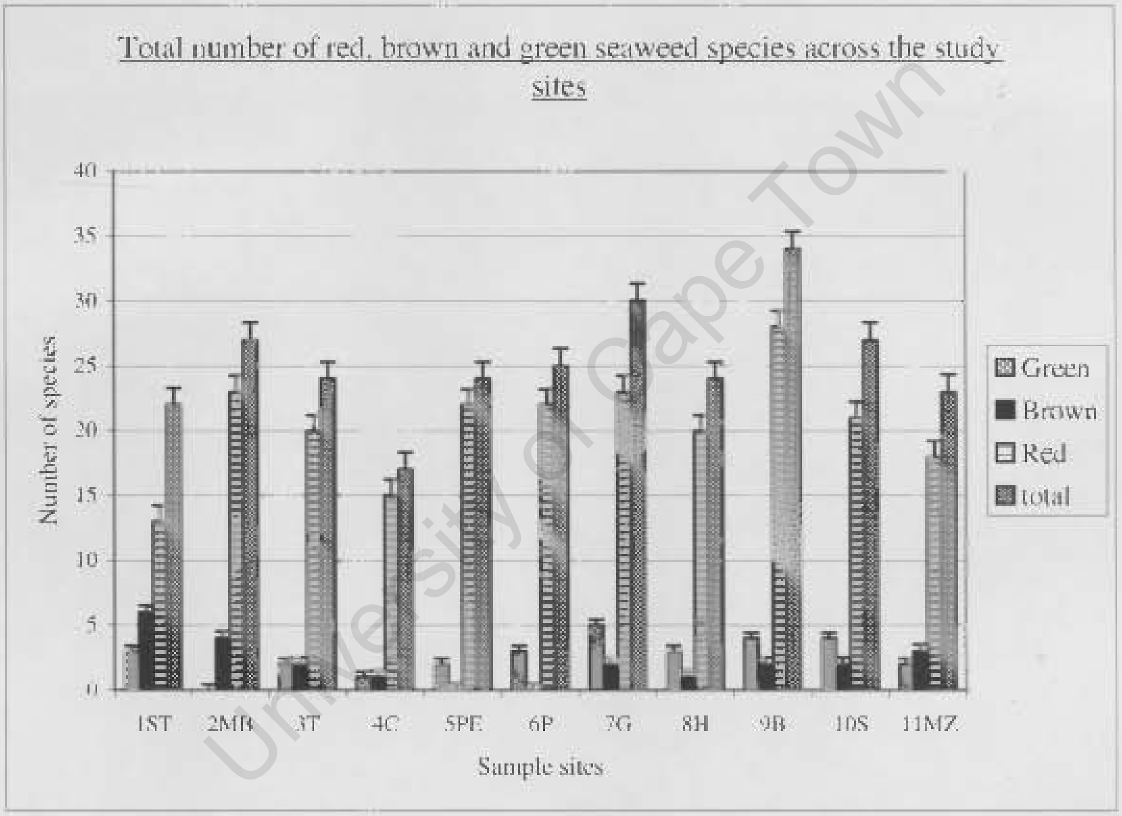

Figure 3.3: The number of red, green and brown algal species as well as the total number of species for the first five quadrats per study site with standard error bars.

At most of the sites there was a greater number of articulated coralline algae than other red algae species (Figure 3.4) however there where many other red species in the data set (as seen in Table 3.1). This suggests that the coralline red algae are more widespread (i.e. they occur at more sites) than the other red algae. Beach Rock had the highest number of species as well as the highest proportion of articulated corallines to other red algae. At this site *Amphiroa* species were abundant especially *A. ephedraea*.

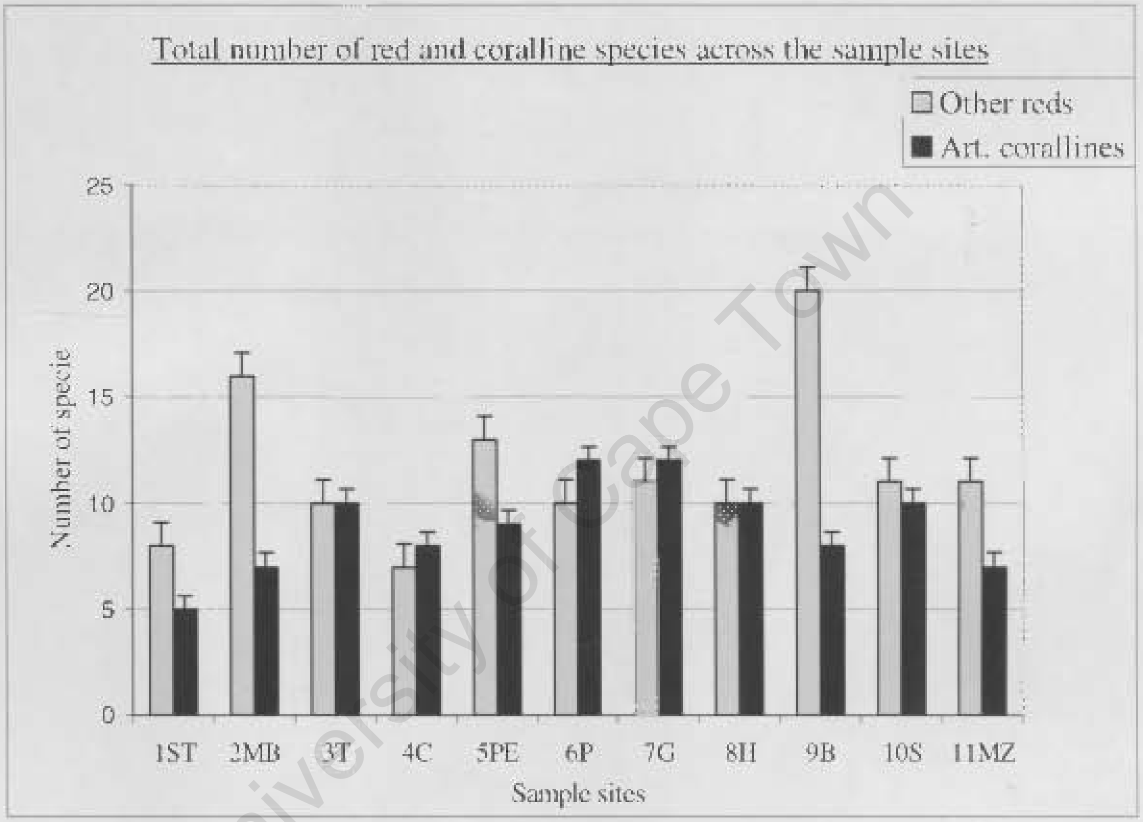

Figure 3.4: The number of coralline and other red algal species with standard error bars for the first five quadrats sampled at each site.

Table 3.3 and 3.4 list the twenty most abundant algal species found in the data set based firstly on the frequency of occurrence as a percentage of the number of quadrats they occurred in, then based on total species biomass. Two of the top three species that were found most frequently were coralline algae, with eleven species in the top 20 (Table 3.3). Eleven species of coralline algae were in the top 20 with regard to biomass, with *Amphiroa ephedraea* first on the list (Table 3.4). However, two green species (namely *Caulerpa filiformis* and *Halimeda cuneata)*, are in the top three with regard to biomass and top five with regard to frequency of occurrence.

Table 3.3: Twenty algal species that occurred most often across the study site using just five quadrats from each site. .

Species	Algal group	Frequency (%)
Arthrocardia carinata	AC	45.5
Arthrocardia corymbosa	AC	45.5
Halimeda cuneata	G	43.6
Haliptilon subulatum	AC	43.6
Caulerpa filiformis	G	41.8
Cheilosporum cultratum subsp. multifidum	AC	40
Amphiroa anceps	AC	38.2
Laurencia flexuosa	R	38.2
Plocamium corallorhiza	R	38.2
Cheilosporum sagittatum	AC	36.4
Amphiroa ephedraea	AC	34.5
Corallina officinalis	AC	34.5
Amphiroa bowerbankii	AC	30.9
Plocamium suhrii	R	29.1
Amphiroa beauvoisii	AC	27.3
Dictyota dichotoma	B	27.3
Champia compressa	R	25.5
Hypnea rosea	R	25.5
Arthrocardia flabellata	AC	21.8
Jania crassa	AC	21.8

Table 3.4: Twenty algal species that were most abundant across the study site using just five quadrats from each site.

Species	Algal group	Total biomass (g)	% of total biomass
Amphiroa ephedraea	AC	7105.38	20.5
Caulerpa filiformis	G	6749.31	19.5
Halimeda cuneata	G	4766.61	13.8
Amphiroa bowerbankii	AC	3966.86	11.5
Amphiroa anceps	AC	2579.49	7.5
Arthrocardia corymbosa	AC	917.18	2.7
Arthrocardia carinata	AC	835.95	2.4
Plocamium corallorhiza	R	706	2.0
Amphiroa beauvoisii	AC	645.53	1.9
Laurencia glomerata	R	535.76	1.5
Gracilaria beckeri	R	398.85	1.2
Laurencia complanata	R	396.06	1.1
Caulerpa holmesiana	G	385.56	1.1
Corallina officinalis	AC	359.42	1.0
Haliptilon subulatum	AC	336.55	1.0
Gelidium abbottiorum	R	309.01	0.9
Jania crassa	AC	283.6	0.8
Sargassum heterophyllum	B	276.14	0.8
Cheilosporum cultratum subsp. multifidum	AC	242.83	0.7
Cheilosporum sagittatum	AC	239.31	0.7

Figure 3.5 is a correlation analysis of the total biomass for each species (g) compared to the frequency of occurrence (as a percentage) of that species. As the frequency increased the species biomass increased significantly (p= 0.000).

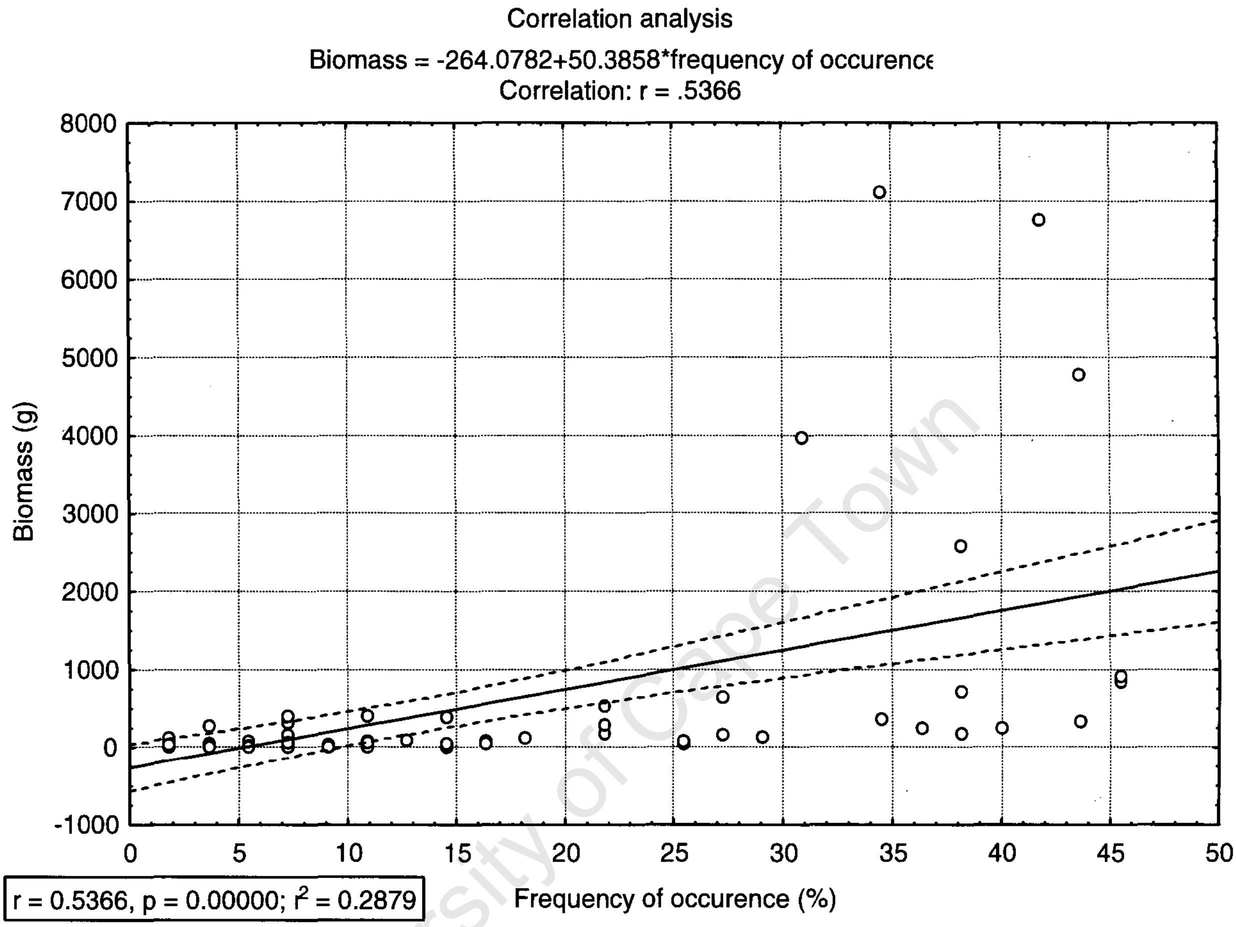

Figure 3.5: Correlation analysis of total species biomass (g) versus the frequency of occurrence (% of quadrats in which species is present) r = 0.5366, p = 0.000.

When depth was compared with biomass in a correlation analysis, there was a negative relationship (Figure 3.6). As depth increased, the algal biomass decreased in a negative relationship that was significant (p= 0.031). Depth was also compared to the number of species present (Figure 3.7). It was found that as depth increased, the number of species did not vary significantly (p= 0.351).

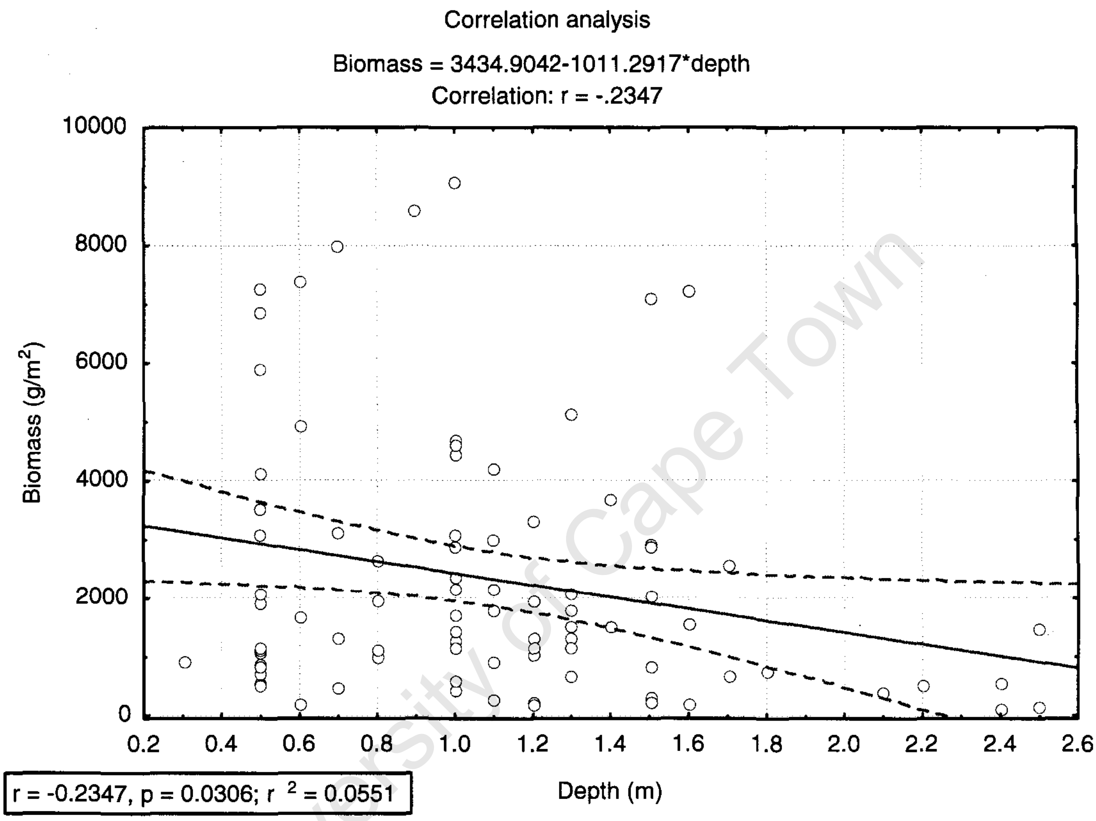

Figure 3.6: Correlation analysis between biomass (g/m^2) and depth (m), r = -0.2347, p = 0.031.

As the slope of the sample surface increased, the biomass did not change significantly (Figure 3.8) ($p= 0.66$). The number of species was also compared to the slope (Figure 3.9) and again there was no significant relationship ($p= 0.157$).

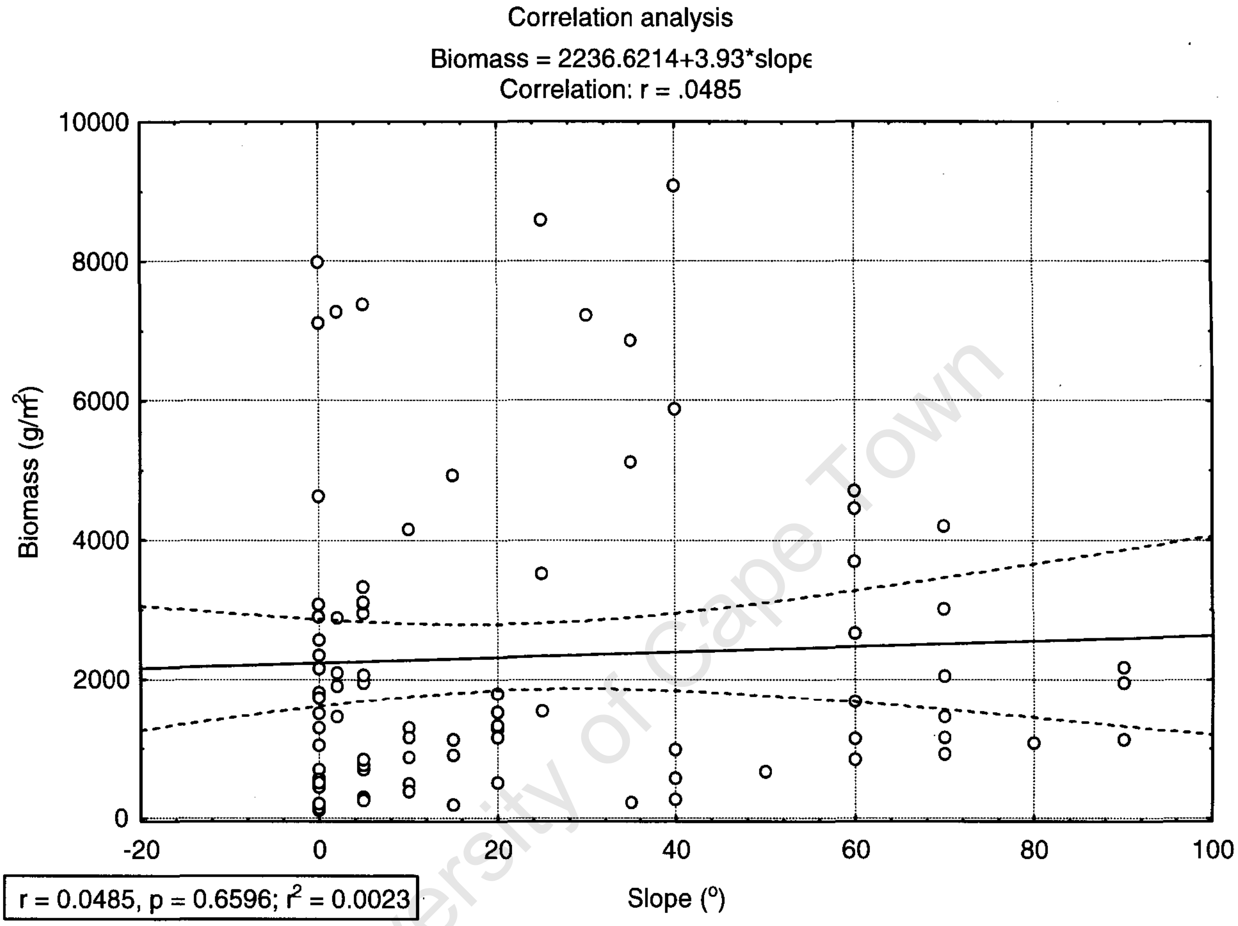

Figure 3.8: Correlation analysis between biomass (g/m^2) and slope (^{O}), $r = 0.0485$, $p = 0.66$.

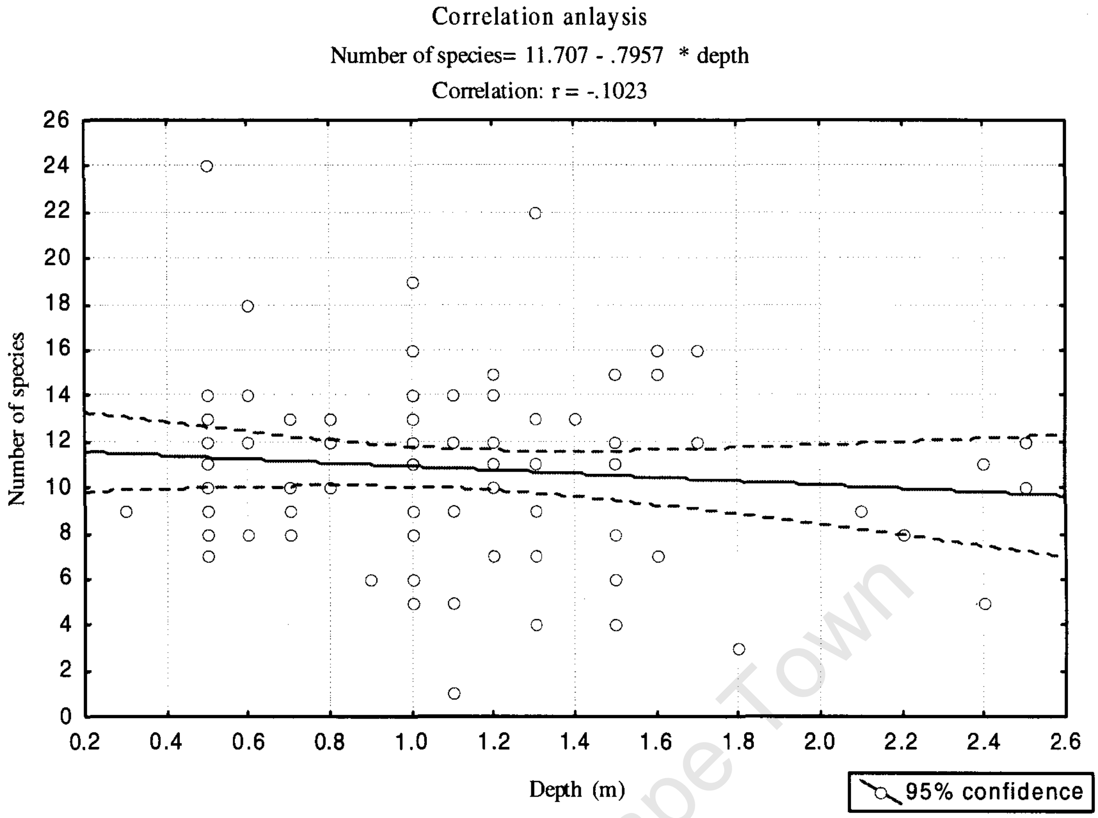

Figure 3.7: Correlation analysis between number of species and depth (m), r = -0.1023, p = 0.351.

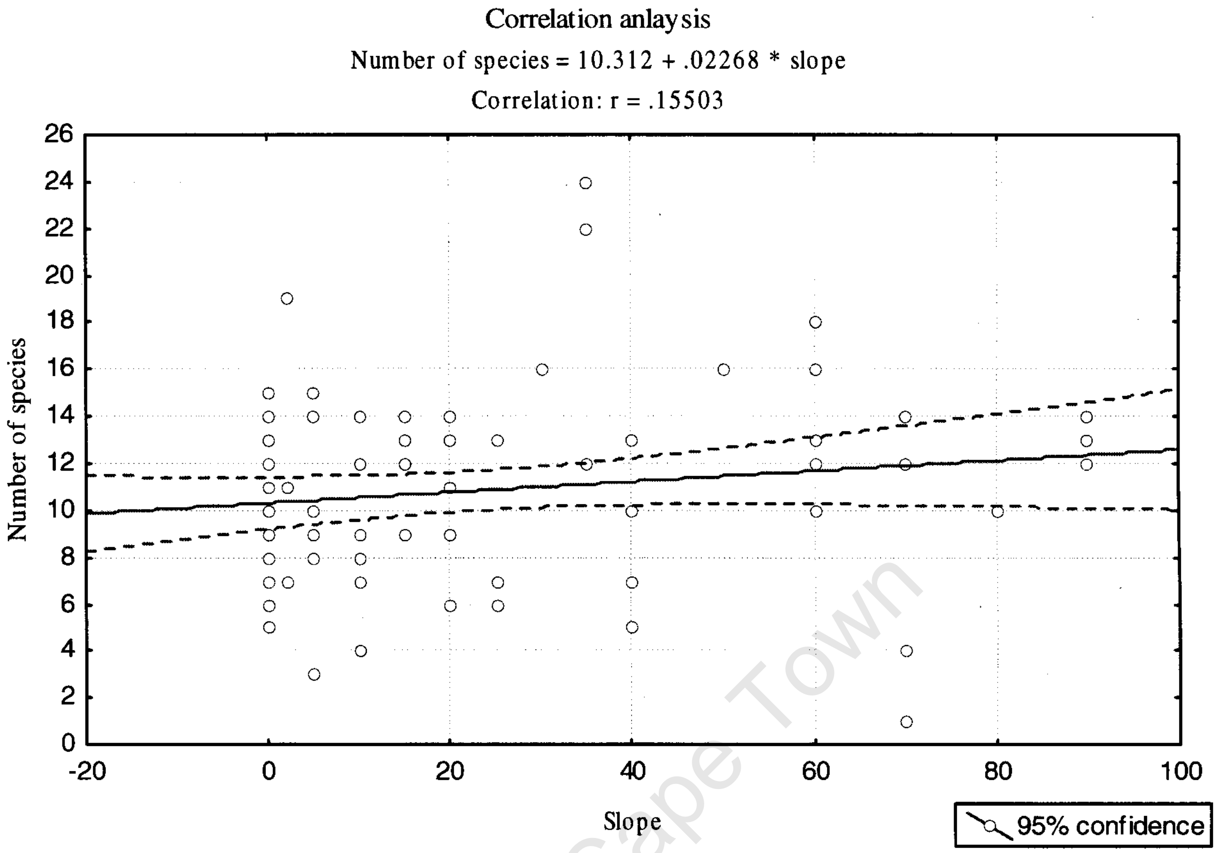

Figure 3.9: Correlation analysis between number of species and slope (^{O}), r = 0.15503, p = 0.157.

The grazers that were found across the study sites, were relatively the same in terms of their type but varied greatly in abundance (Table 3.5). Although they were not identified to species level, they still provide interesting information at the level of broad groups.

Table 3.5: The total number of grazers found at each site that were included in the correlation analysis.

Grazer	ST	MB	T	C	PE	P	G	H	B	S	MZ
Chiton	0	3	6	0	0	2	8	3	2	1	8
Limpet	1	1	4	2	0	3	0	9	0	1	0
Sea hare	0	0	1	0	9	0	0	0	0	0	0
Urchin	0	0	12	61	15	11	2	22	0	0	0
Winkle	13	7	37	28	23	11	4	24	41	12	11
TOTAL	14	11	60	91	47	27	14	58	43	14	19

The number of grazers present was compared to biomass (Figure 3.10) and the number of species (Figure 3.11). There was found to be no significant relationship between number of grazers present and either seaweed biomass (Figure 3.10) or number of species (Figure 3.11) (p= 0.228 and p= 0.382 respectively).

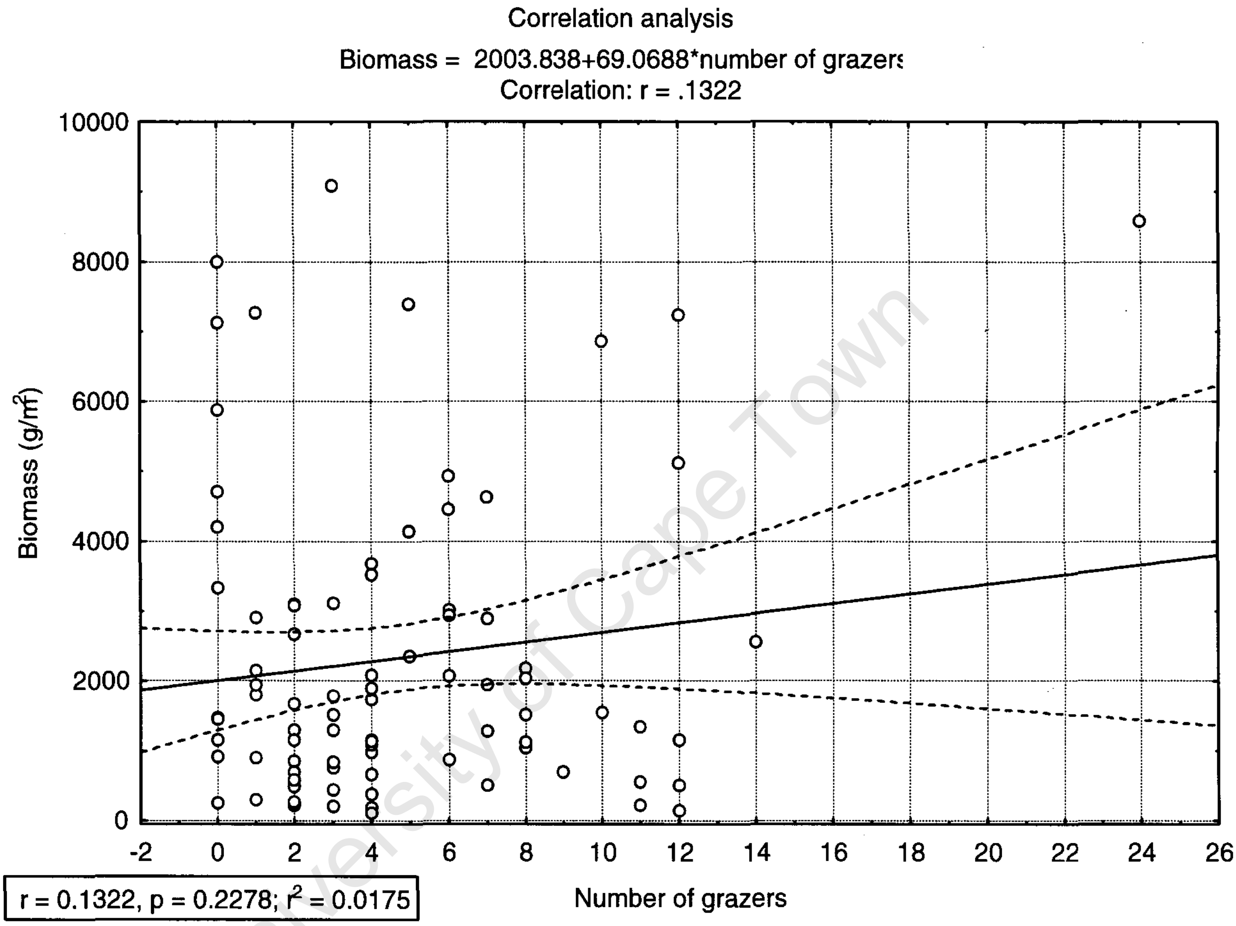

Figure 3.10: Correlation analysis between seaweed biomass (g/m^2) and the number of grazers in each quadrat, r = 0.1322, p = 0.228.

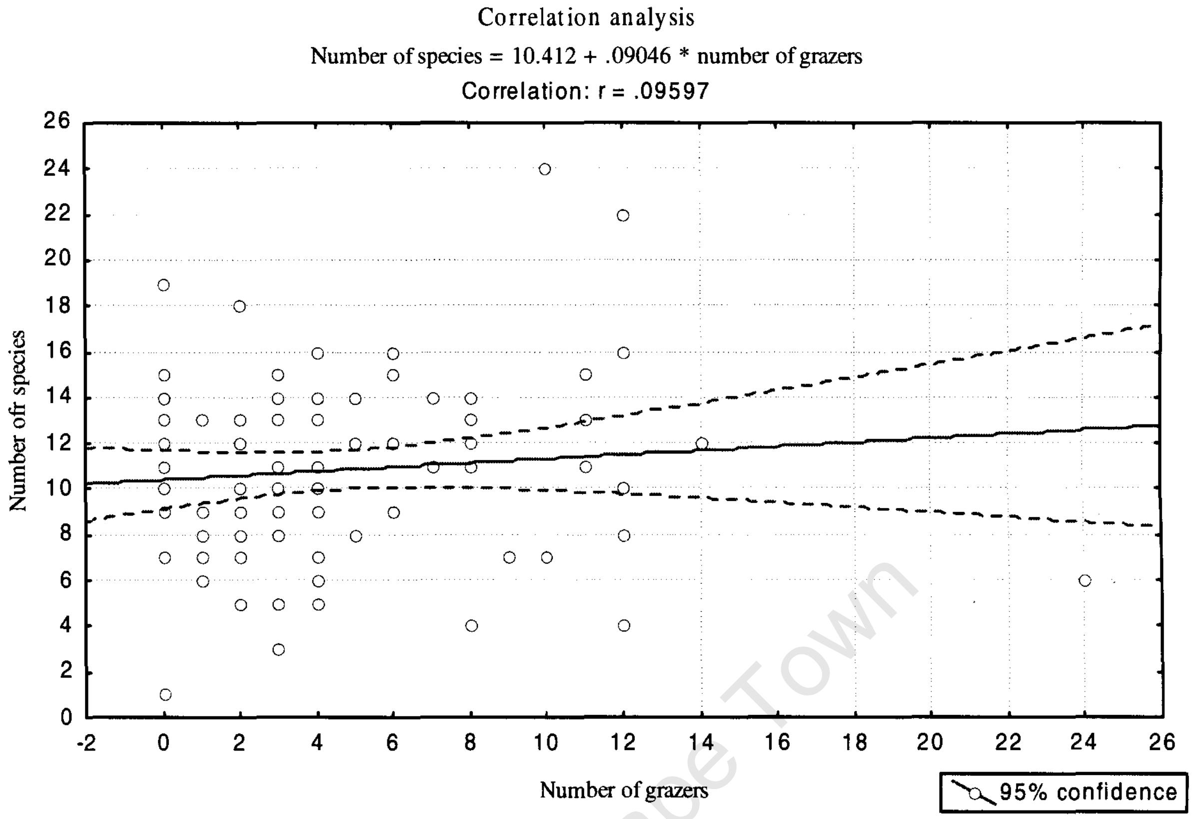

Figure 3.11: Correlation analysis between the number of seaweed species and the number of grazers in each quadrat, r = 0.09597, p = 0.382.

Figure 3.12 is a correlation analysis between the number of grazers in each quadrat and the sample depth. There is a significant positive relationship between these two variables (p = 0.033) suggesting that as the depth increases the number of grazers present also increases, within the depth range 0.2 to 2.5m.

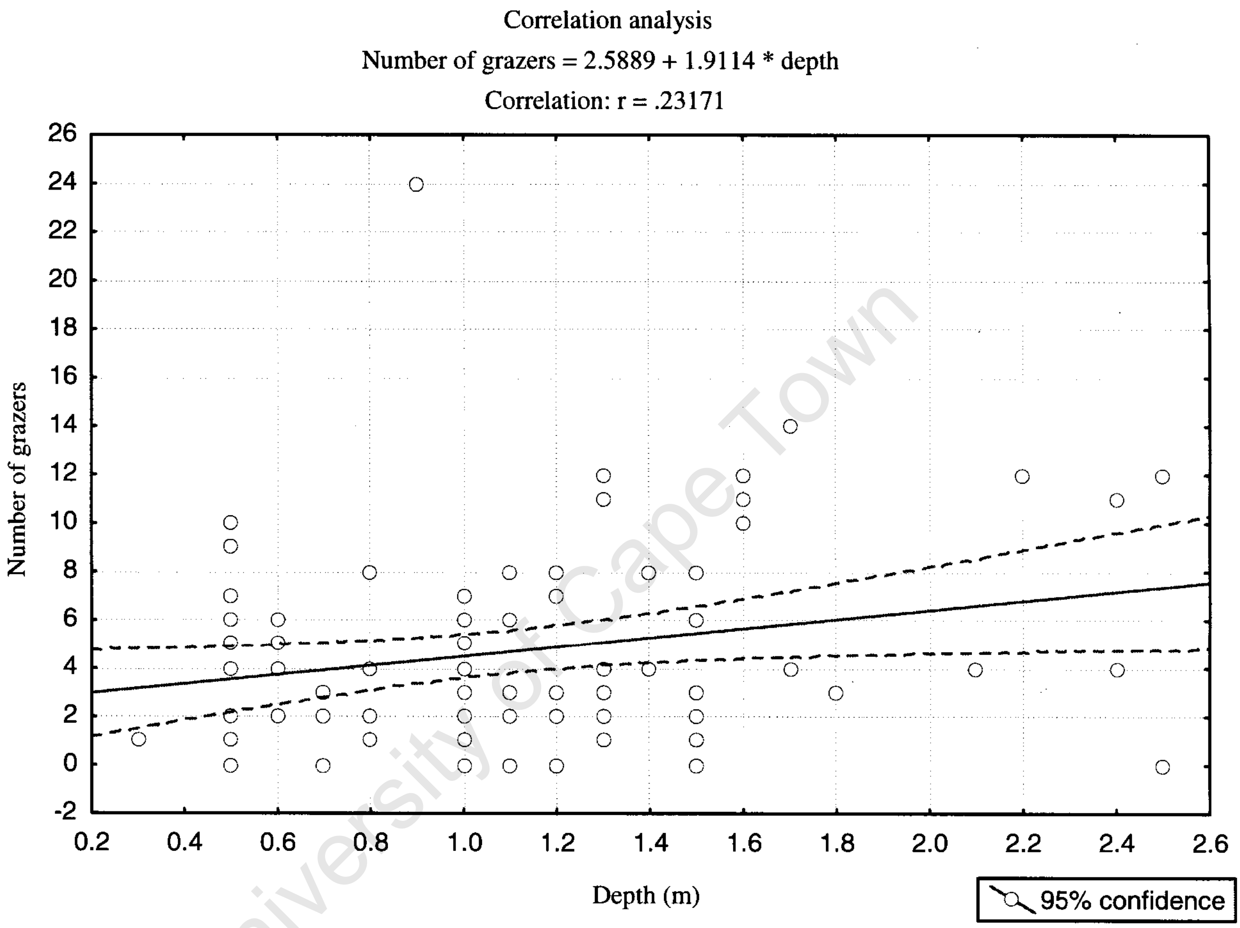

Figure 3.12: Correlation analysis between number of grazers and the depth (m), r = 0.2317, p = 0.033.

The estimated mean annual temperature for the eleven sites varied considerably, as seen in Table 3.6. The mean annual temperature increases as one moves easterly around the coast, away from Cape Agulhas. The western sites have the highest temperature ranges, especially Still Bay and Mossel Bay (7.4°C and 6.9°C respectively), with range decreasing towards the eastern sites, except for Mzamba where the temperature range increases again (4.7°C). There is a large increase in mean, minimum and maximum temperatures between Haga Haga and Beach Rock, with only a slight increase in range.

Table 3.6: The sea surface temperature (mean annual, minimum, maximum and the temperature range) for the 11 study sites. Sites with * besides them are those for which the temperature data was interpolated rather than obtained from sites specified in Bolton (1986).

	MEAN (°C)	MINIMUM (°C)	MAXIMUM (°C)	RANGE (°C)
Still Bay	17.3	13.8	21.2	7.4
Mossel Bay*	17.2	14.0	20.9	6.9
Tsitsikamma*	17.2	14.8	20.3	5.5
Cape St. Francis*	17.8	15.2	20.6	5.4
Port Elizabeth	18.2	15.8	20.8	5.0
Port Alfred*	18.0	16.3	19.6	3.3
Glen Muir*	18.3	16.7	19.5	2.8
Haga Haga*	18.4	16.7	19.6	2.9
Beach Rock*	20.8	19.1	22.1	3.0
Silaka*	20.9	19.1	22.2	3.1
Mzamba*	21.2	19.0	23.7	4.7

The mean annual sea surface temperature for each of the eleven sites was compared with the average biomass (Figure 3.13) and the number of species (Figure 3.14) but no significant relationship was found.

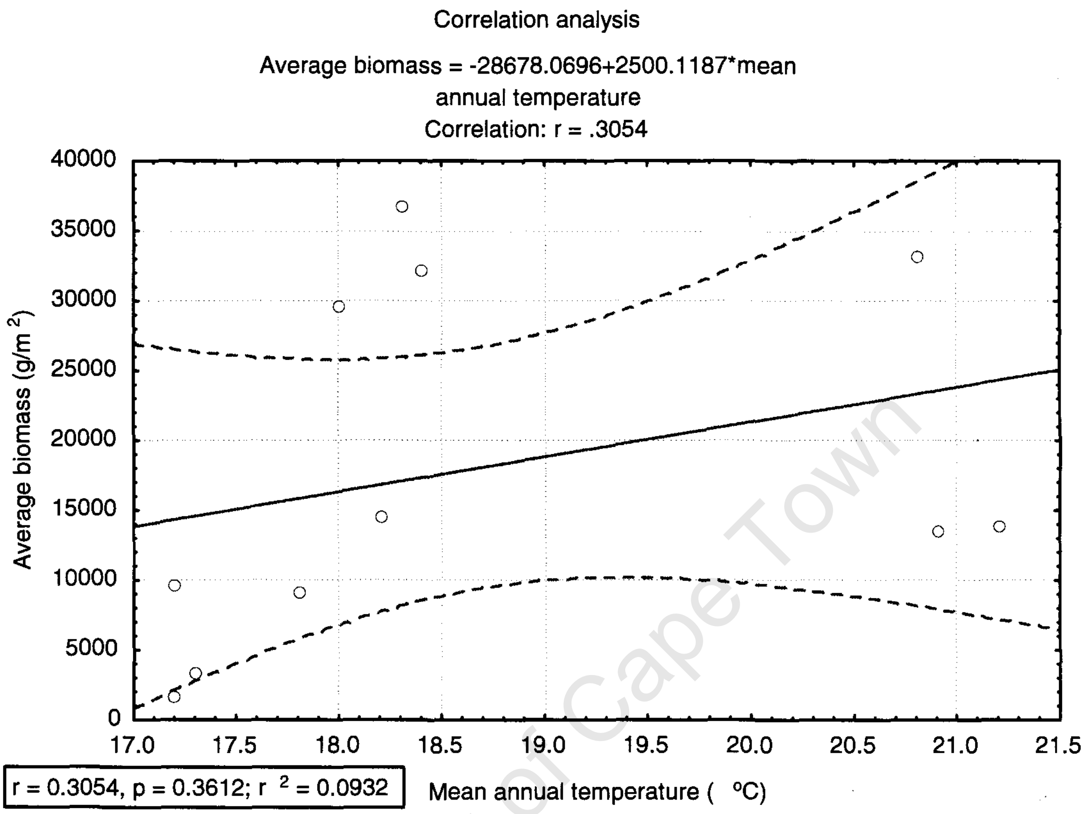

Figure 3.13: Correlation analysis between average biomass (g/m^2) and the mean annual sea surface temperature (°C), r = 0.3054, p = 0.36.

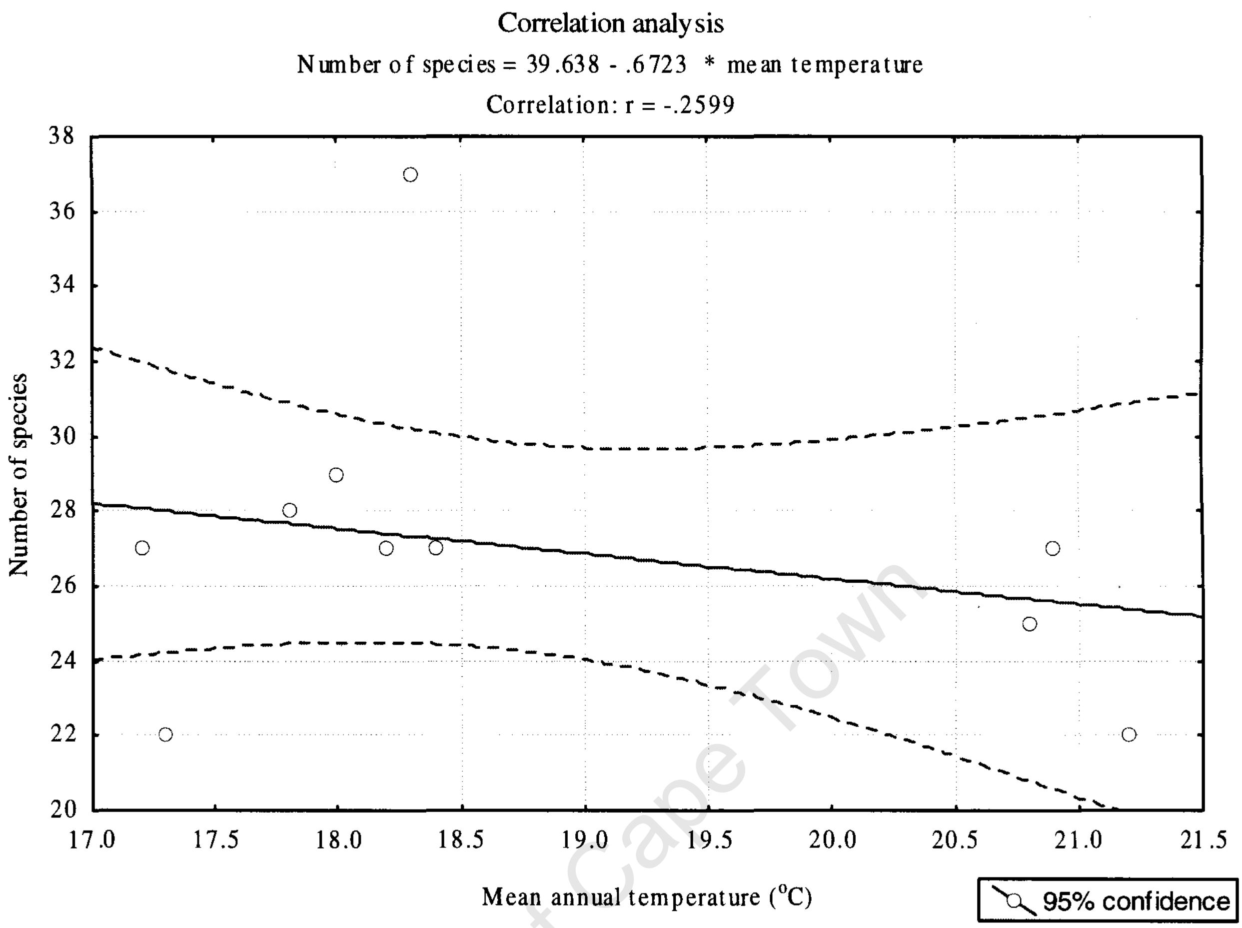

Figure 3.14: Correlation analysis between number of species and the mean annual sea surface temperature (°C), $r = -0.2599$, $p = 0.440$.

The biomass and number of species was also compared with the sea surface temperature range (Figures 3.15 and 3.16). When the temperature range increased the biomass decreased in a negative relationship that was found to be significant (p=0.0003). The relationship between the number of species and the range of sea surface temperature was found not to be significant (p= 0.144).

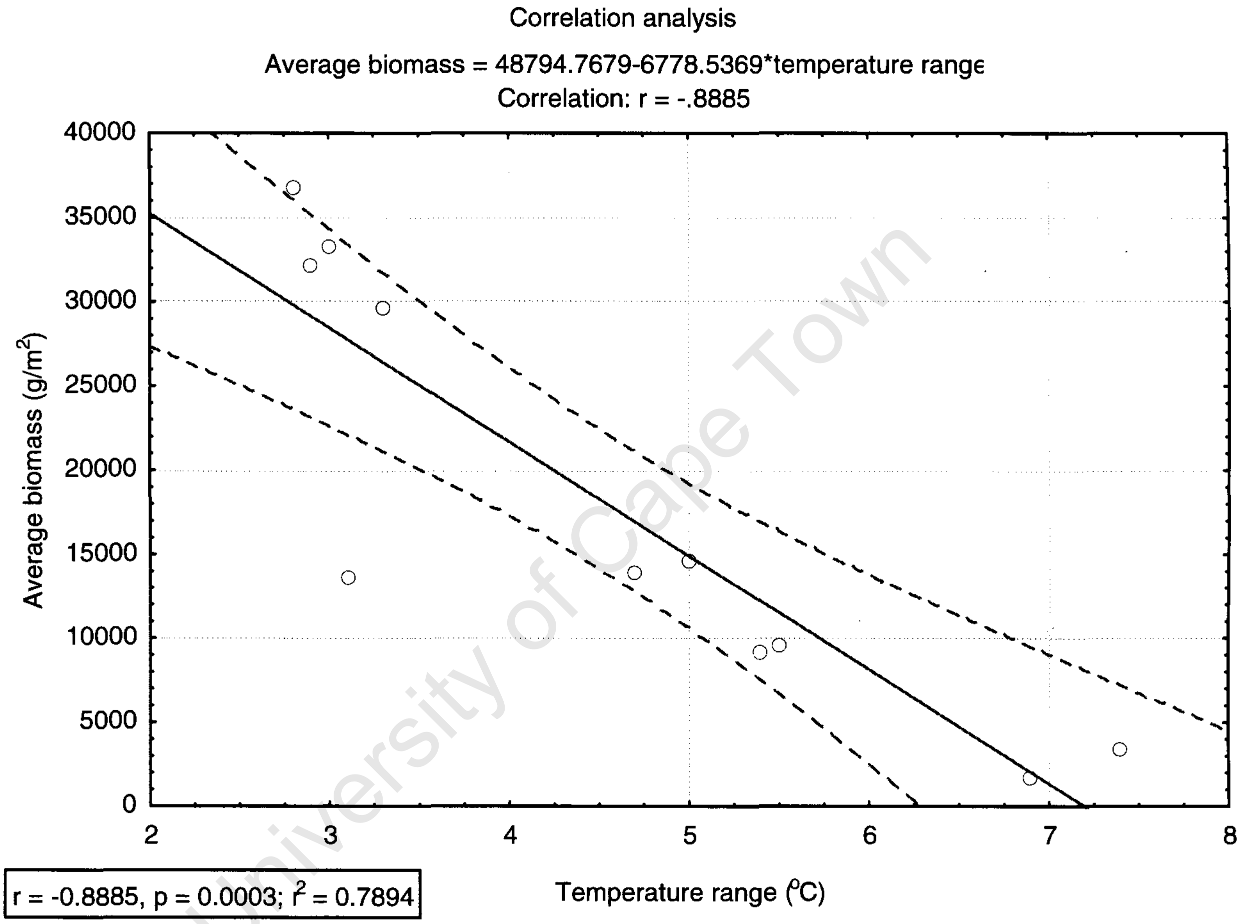

Figure 3.15: Correlation analysis between average biomass (g/m^2) and sea surface temperature range (°C), r = -0.8885, p = 0.0003.

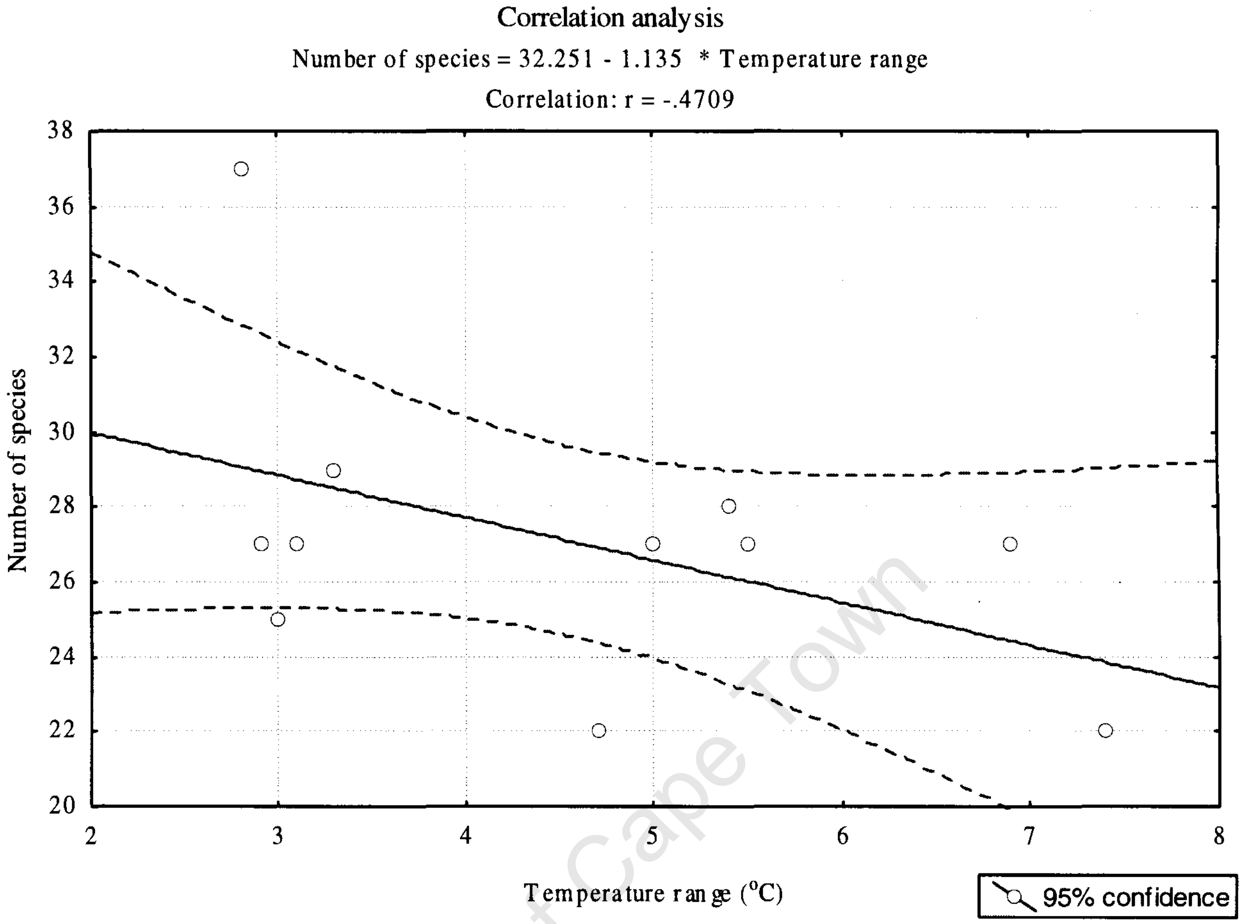

Figure 3.16: Correlation analysis between the number of species and sea surface temperature range (°C), r = -0.4709, p = 0.144.

Figure 3.17 is the correlation analysis between mean annual temperature and temperature range for each of the 11 study sites using estimated data. It shows that although there is a negative relationship between these two variables (i.e. as temperature range increases, mean annual temperature decreases) the relationship is not significant (p=0.082).

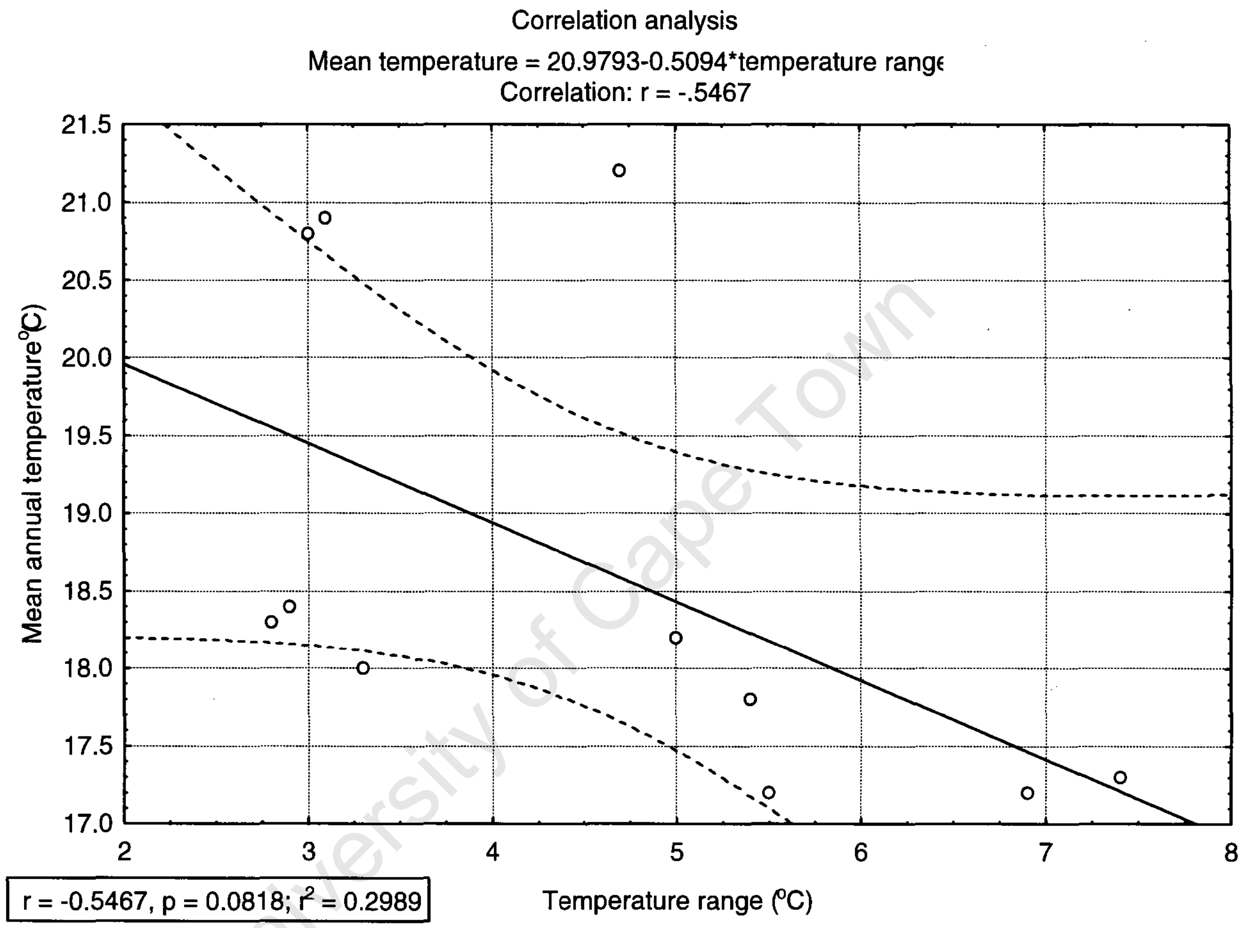

Figure 3.17: Correlation analysis between mean annual temperature and temperature range $r = -.05467$, $p = 0.0818$.

There was found to be no significant relationship between the biomass and the number of species (Figure 3.18). As the biomass increased the number of species (or the species richness) remained relatively unchanged (p= 0.873).

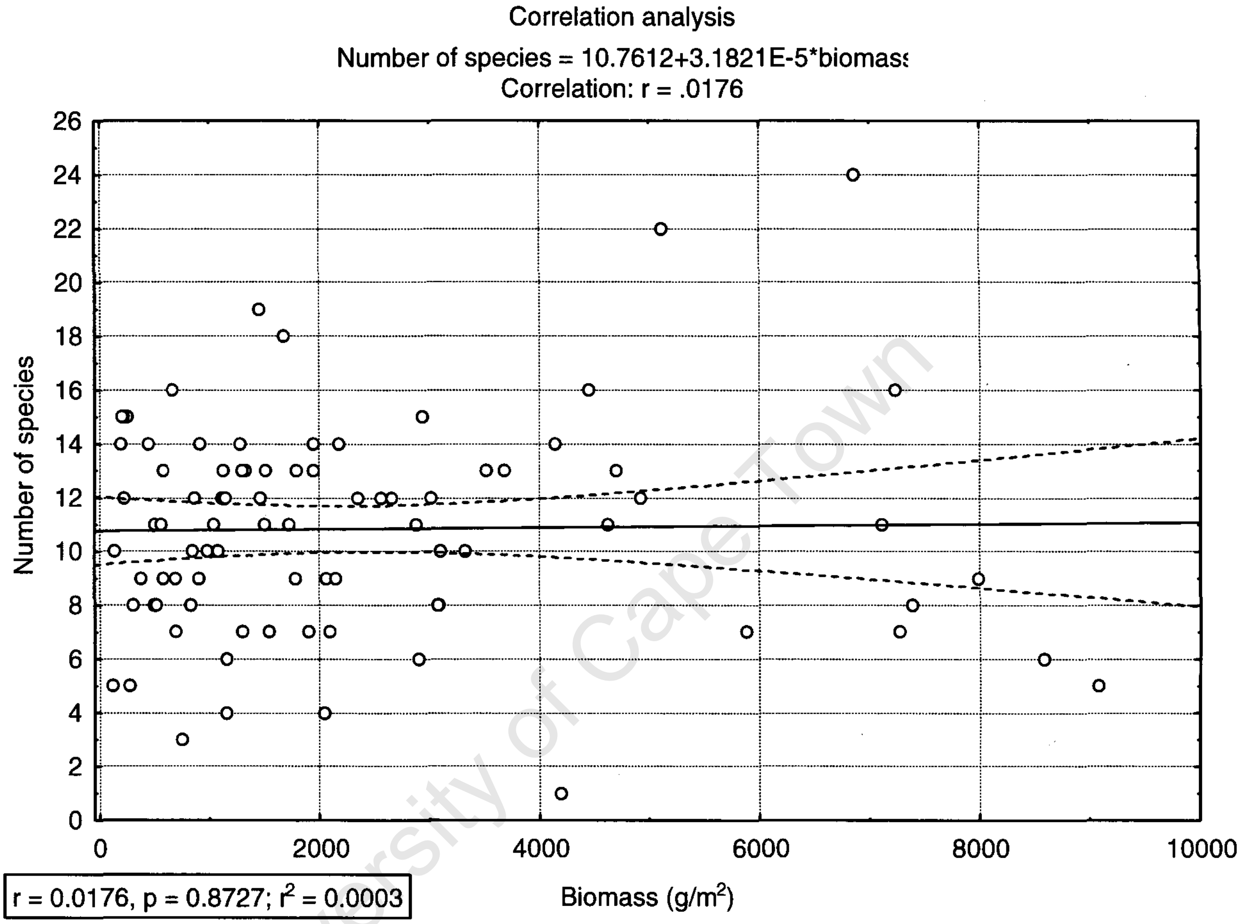

Figure 3.18: Correlation analysis between the number of species and biomass (g/m^2), r = 0.0176, p = 0.873.

Biogeographical analysis

Figures 3.19 and 3.20, the DECORANA plots for samples and species respectively, are based on species presence/absence data. Figure 3.18 shows no real clusters or grouping, but samples from different sites are distributed along axis one roughly on a biogeographical gradient. This gradient visible along axis one places western sites on the right of the plot and the eastern sites on the left of the plot with approximately 50% of the variation explained or attributed to the gradient on this axis. Axis two of this plot separates the three sites in the extreme east from one another i.e. Mzamba from Silaka and Beach Rock. The separation shown in Figure 3.19 is a result of rather different species occurring at Mzamba compared with at Silaka and Beach Rock (Figure 3.20). Mzamba is characterised by species such as *Inkyuleea beckerii* and *Martensia elegans* (species number 58 and 67) plus Amphiroa *bowerbankii, Dictyomenia stephensonii* and *Metamastophora flabellata*. Silaka and Beach Rock are characterised by *Botryocladia madagascariensis, Cheilosporum proliferum, Corallina sp1, Dictyota dichotoma var. intricate, Laurencia complanata, Peyssonnelia capensis, Rhodymeniaceae sp., Spyridia horridula, Stypopodium zonale* and *Valonia macrophysa* (Figure 3.20).

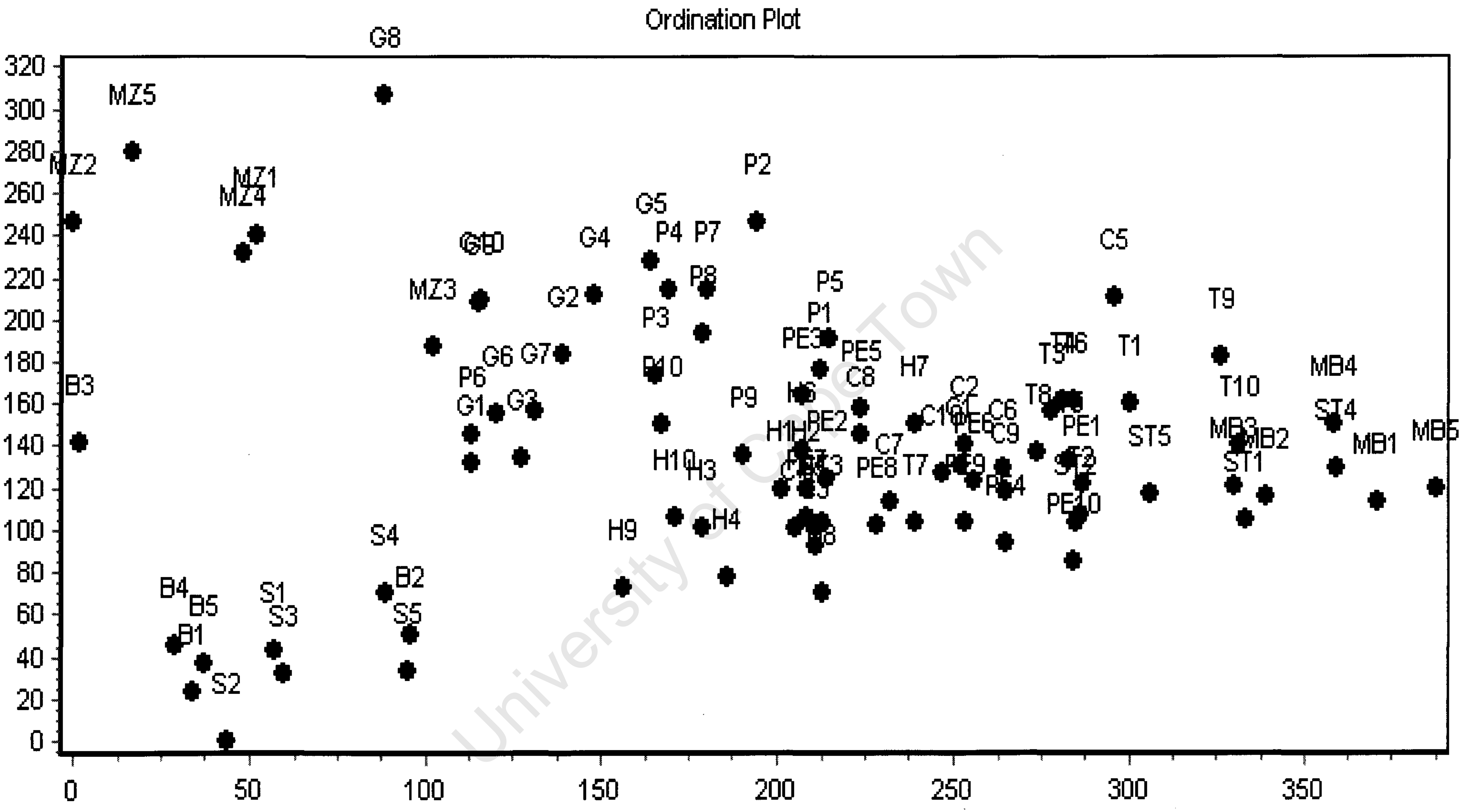

Figure 3.19: DECORANA for samples using presence/absence data. The eigenvalue for axis 1 is 0.5123353004 and for axis 2 is 0.3166119158.

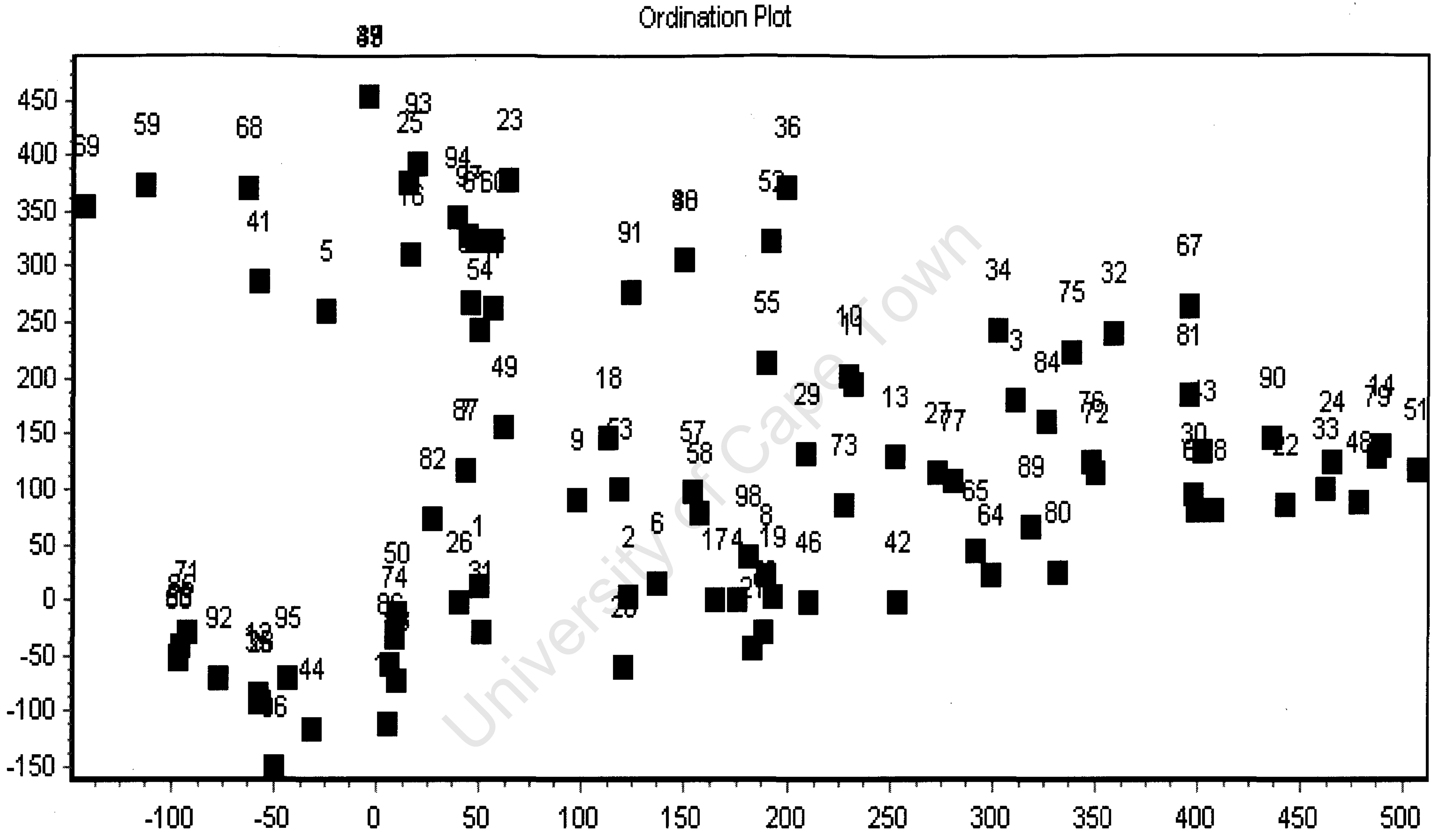

Figure 3.20: DECORANA for the species using presence/absence data. The eigenvalue for axis 1 is 0.5123353004 and for axis 2 is 0.3166119158.

Figure 3.21 and 3.22 are the DECORANA plots for samples and species respectively, based on biomass data. Figure 3.20 separates Still Bay on the one side of the plot and Haga Haga and Glen Muir on the other. This separation is along axis one and could be attributed to the difference in temperature range between these sample sites, with Still Bay having a high temperature range (7.4°C) and the latter two sites having a relatively low temperature range (2.9°C and 2.8°C respectively). Therefore axis one could be considered as a temperature range gradient explaining approximately 80% of the variation found between sample sites. Figure 3.22 shows the species that form separate communities and those that characterise the above-mentioned communities. The Haga Haga and Glen Muir sites are characterised by species *Acrosorium maculatum, Apoglossum spathulatum, Caulerpa filiformis, Caulerpa holmesiana, Caulerpa zeyheri, Chaetomorpha spiralis, Corallina sp, Falkenbergia rufolanosa, Gelidium pteridifolium, Halimeda cuneata, Hypnea tenuis, Inkyuleea beckeri, Jania intermedia, Pterosiphonia cloiophylla, and Stypopodium multipartitum.*

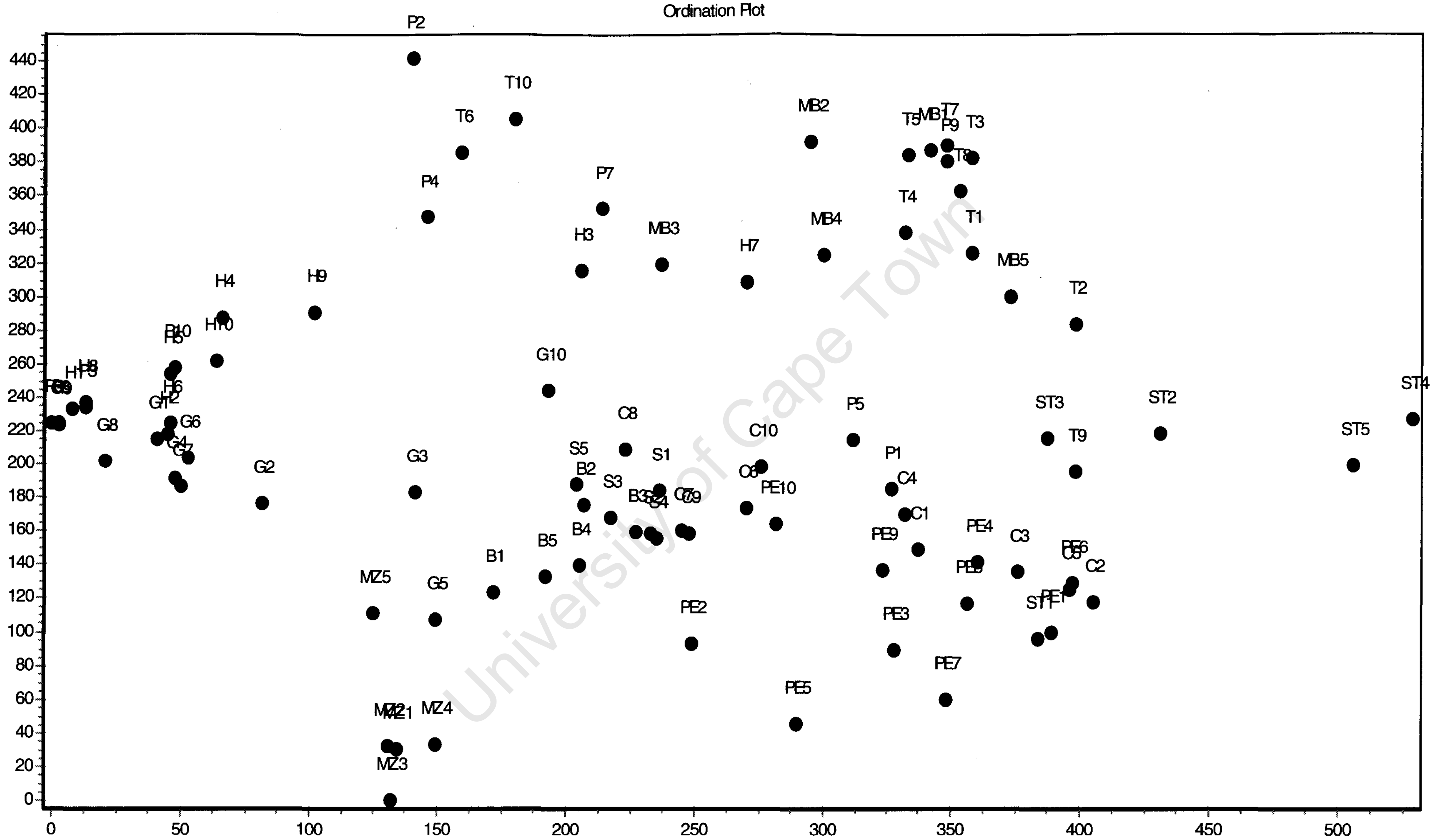

Figure 3.21: DECORANA for samples using biomass data. The eigenvalue for axis 1 is 0.8015127778 and for axis 2 is 0.5824317932.

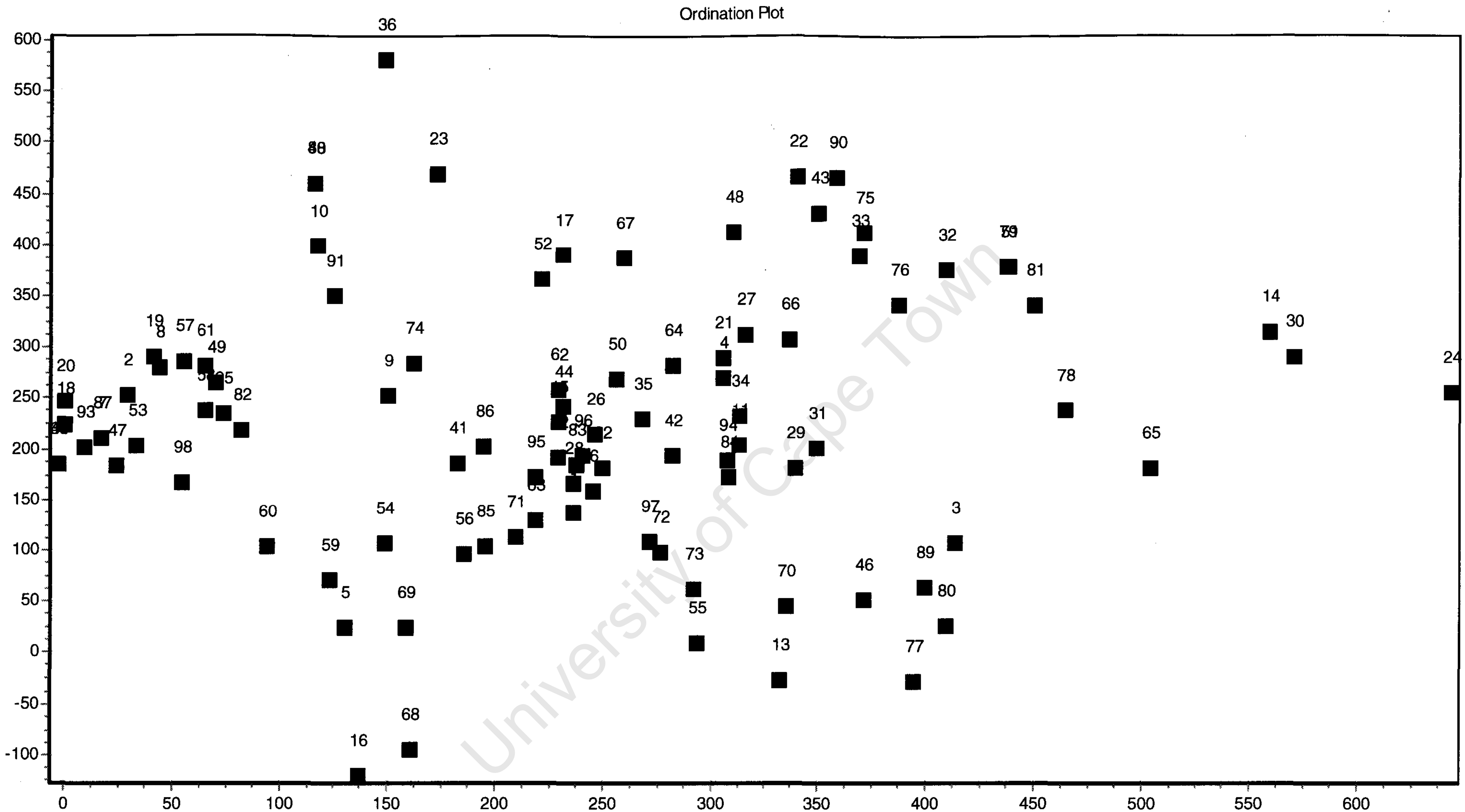

Figure 3.22: DECORANA for the species using biomass data. The eigenvalue for axis 1 is 0.8015127778 and for axis 2 is 0.5824317932.

Figure 3.23 is the canonical correspondence analyses using the presence/absence data compared to the environmental data. It shows the impact that minimum monthly temperature, maximum monthly temperature and the temperature range has on the different study sites. Temperature range and minimum temperature values are the most important factors affecting the presence/absence or species richness. The minimum temperature distinguished or differentiated the Mzamba, Silaka and Beach Rock communities from the more easterly sites, and the temperature range affected the Still Bay and Mossel Bay communities.

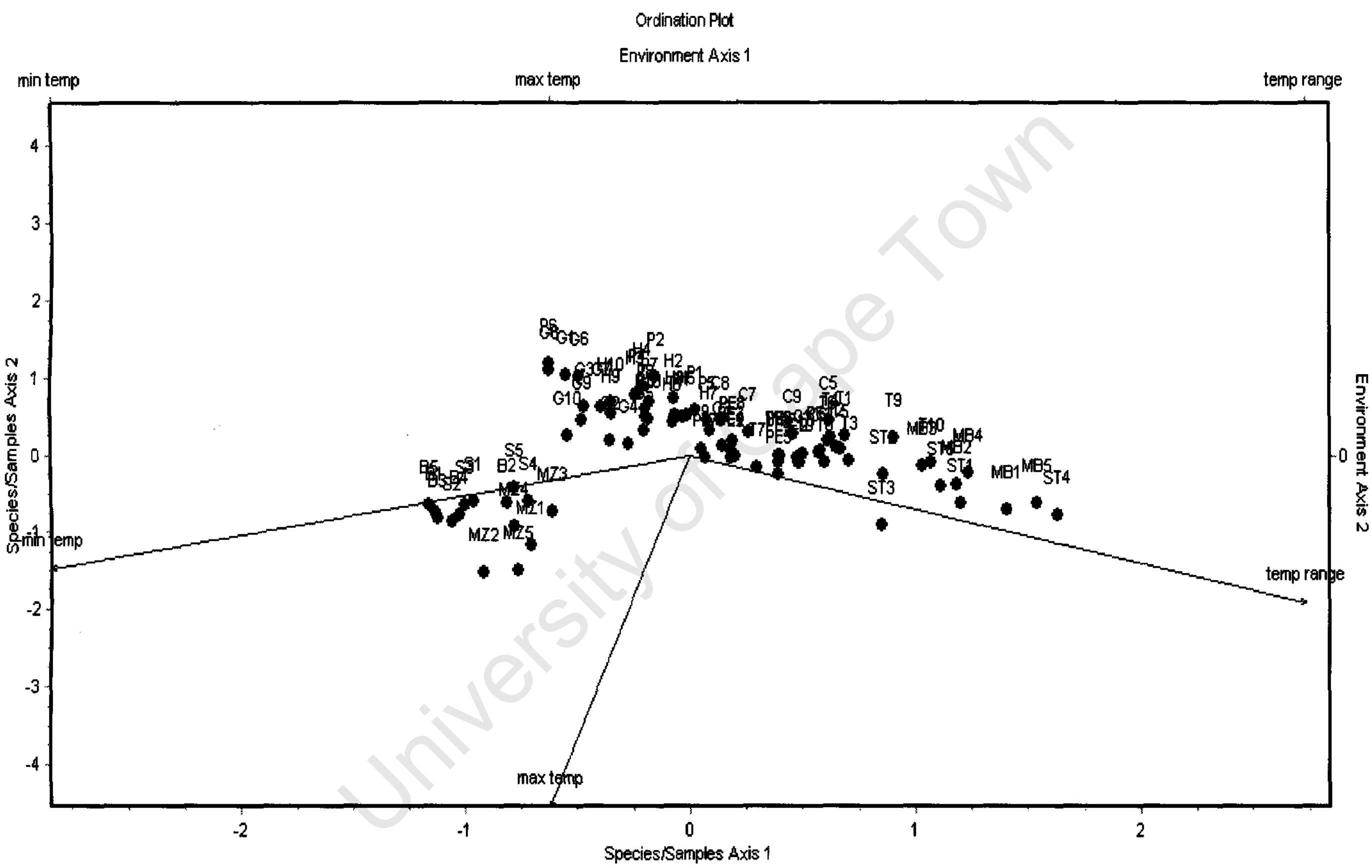

Figure 3.23: Canonical correlation analysis of presence/absence data with the sites at species centroids. The environmental data used were minimum monthly temperature, maximum monthly temperature and temperature range. The eigenvalue for the x-axis is 0.49 and for the y-axis is 0.26.

Figure 3.24 is the canonical correspondence analysis of the biomass data constrained by the minimum and maximum monthly temperature as well as with the temperature range. Here, the maximum temperature is most important especially for the Mzamba and Silaka and the minimum temperature mainly affects the Beach Rock sites. The temperature range was seen to cause the most variation with the Still Bay sites as compared to the other sites, and this could be attributed to the high temperature range here (7.4°C).

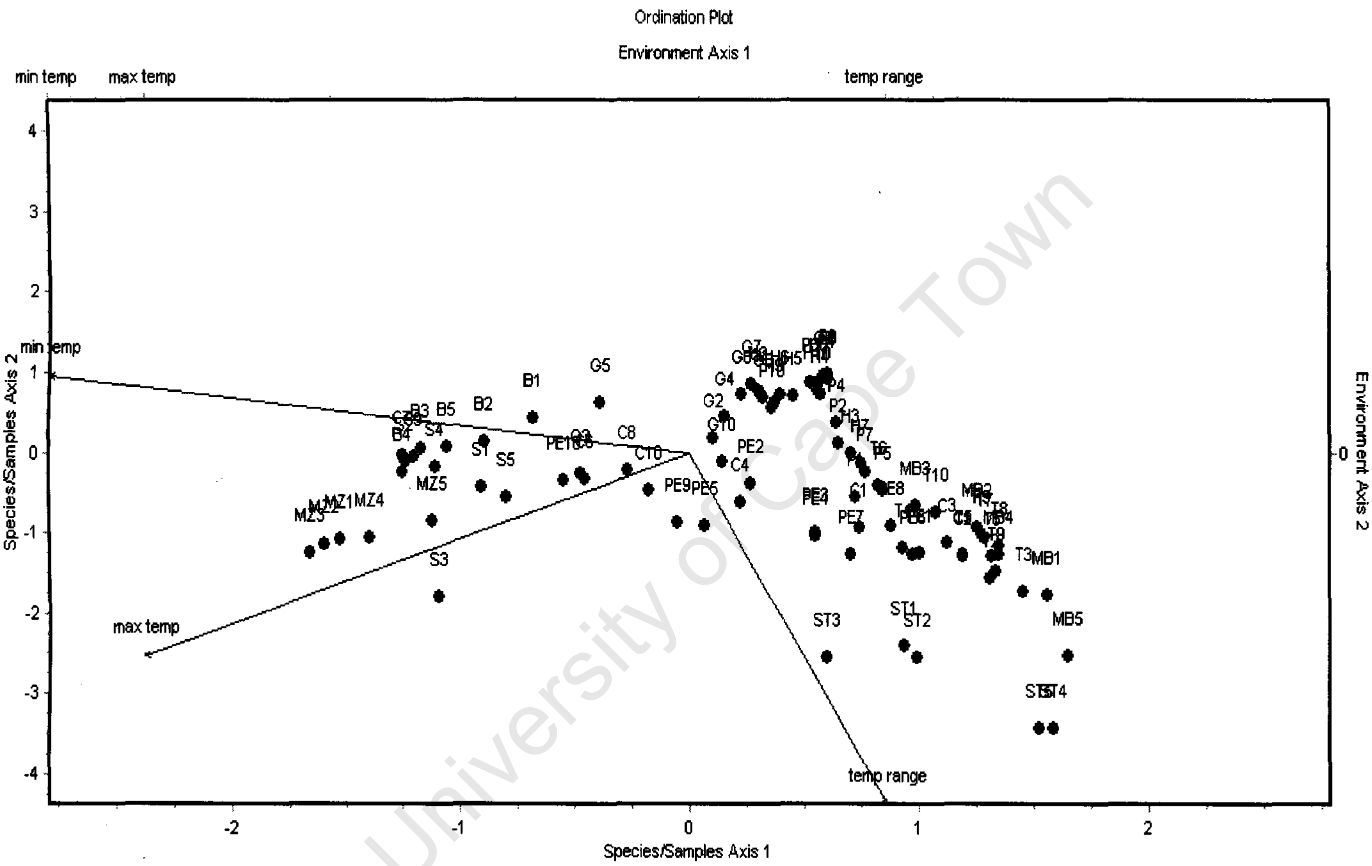

Figure 3.24: Canonical correlation analysis of biomass data with the sites at species centroids. The environmental data used was minimum monthly temperature, maximum monthly temperature and temperature range. The eigenvalue for the x-axis is 1.51 and for the y-axis is 0.44.

Figure 3.25 and 3.26 are the agglomerative cluster analysis (hierarchical) based on presence/absence and biomass data respectively. In Figure 3.24 the first division separates P6 (the sixth quadrat sampled at Port Alfred) from all the other samples. The second division separates Beach Rock, Silaka and Mzamba (i.e. the easterly sites) from the westerly sites. The third division separates Still Bay from the other sites and the next division separates Port Elizabeth and sites to the west from Port Alfred and sites to the east. Samples from Cape St. Francis occur in both these latter two groups, however it is near to Port Elizabeth so some fit in the western group while other samples are more similar in their flora composition to the other more easterly sites.

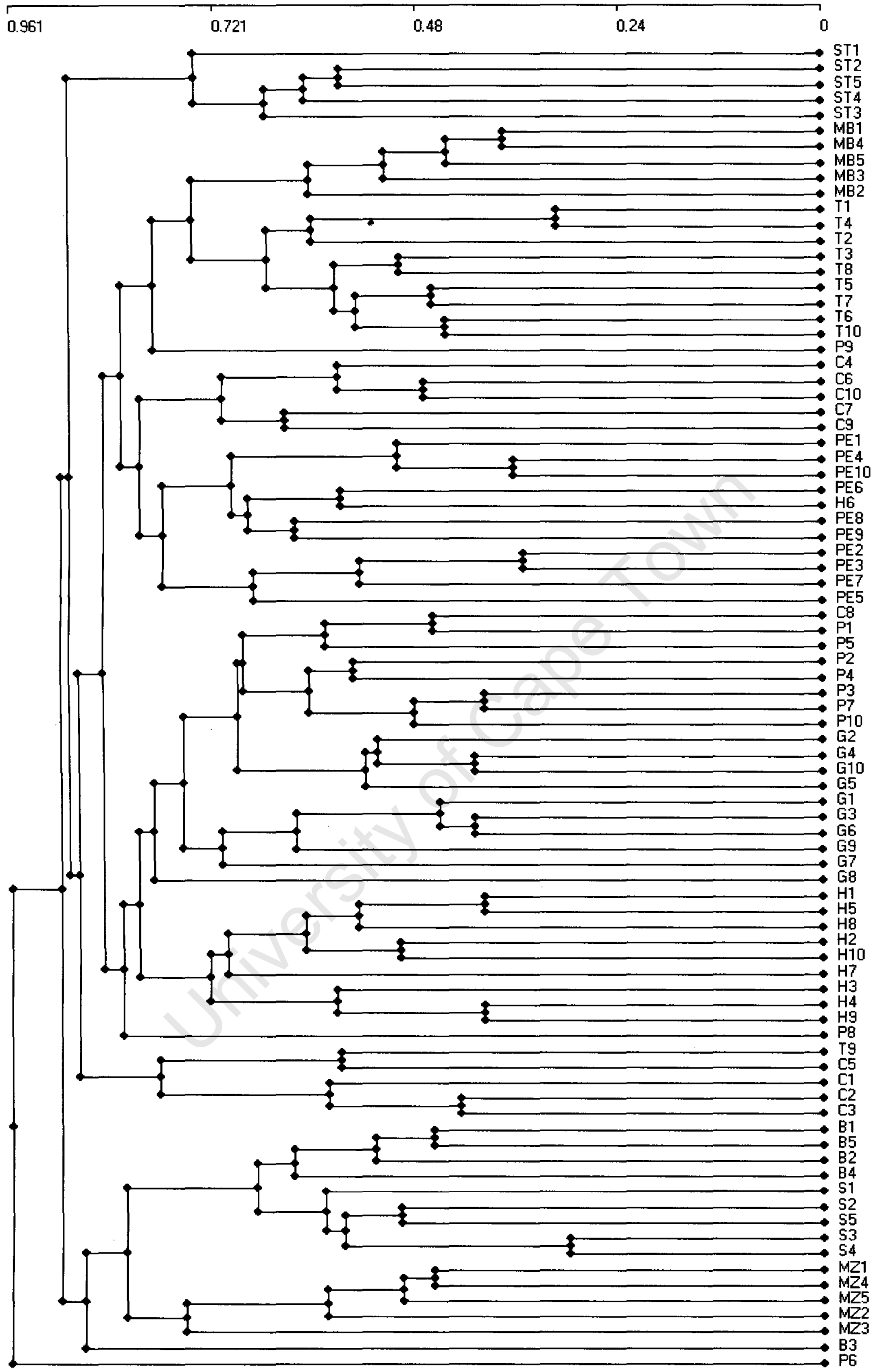

Figure 3.25: Cluster analysis of presence/absence data for samples using Jaccard similarity index: average linkage of dissimilarity.

Figure 3.26 (the biomass data) shows a lot more divisions between the sample sites. The first division separates B3 (the third quadrat sampled at Beach Rock) from the other sample and the second division separates B1 and G5 (the first Beach Rock and fifth Glen Muir samples) from the other samples. There are many divisions of this nature separating a few samples from the others but the first major grouping clusters some Beach Rock and Silaka samples together (eastern sites), four of the five Mzamba samples together and then most of the westerly sites are grouped together (i.e. Still Bay, Mossel Bay, Tsitsikamma, Port Elizabeth and Cape St. Francis).

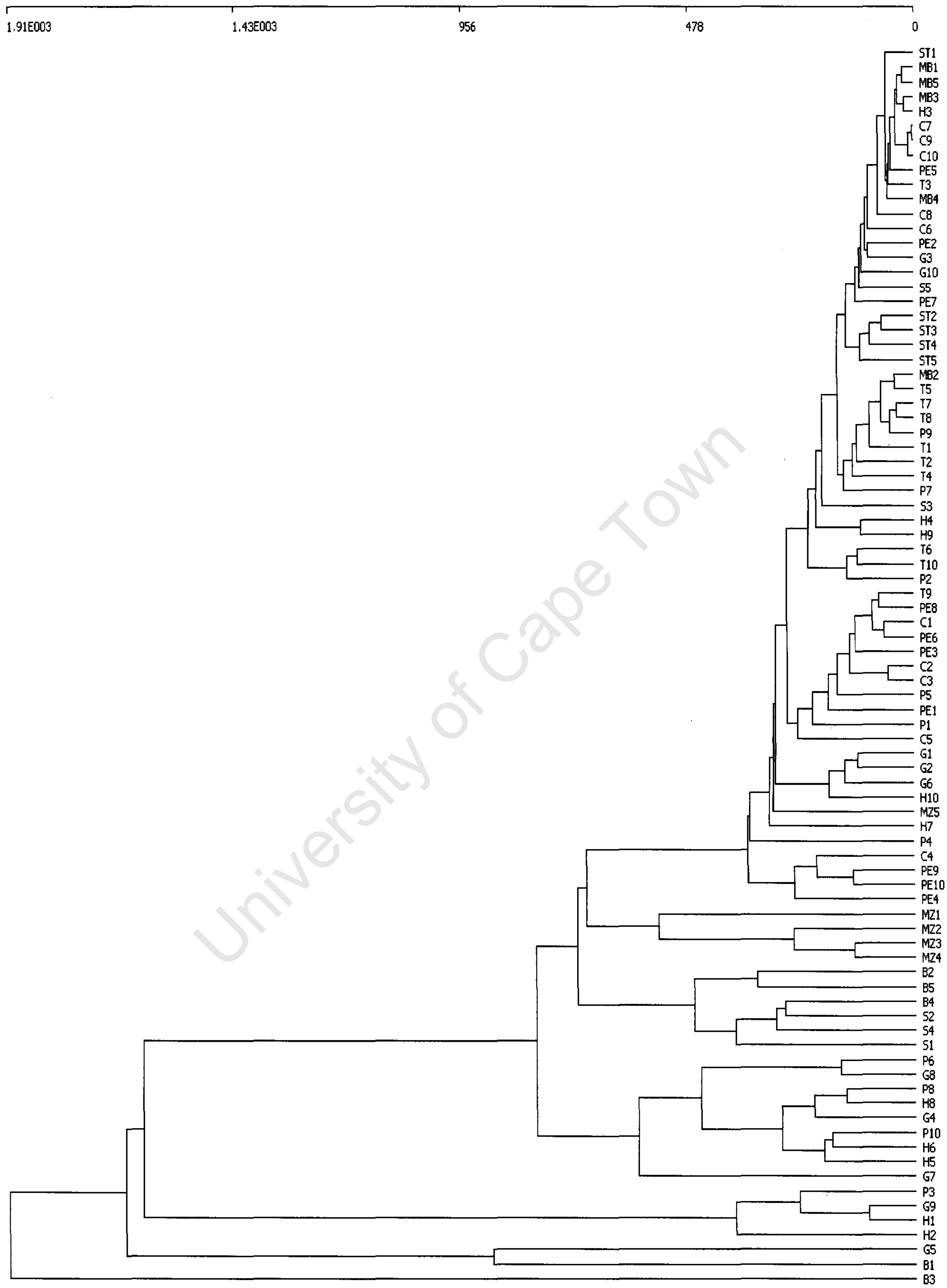

Figure 3.26: Cluster analysis of biomass for the samples using Euclidean distance: average linkage of dissimilarity .

The coastline of South Africa was divided into 50km sections for the biogeographical analysis of seaweed distribution by Bolton & Stegenga (2002). An analysis of the updated collection lists for the south coast (Bolton, Anderson and Stegenga unpublished) is shown in figure 3.27. It can be seen that along the south coast of South Africa there is a primary division (seaweed species presence/absence) in the region of Keiskamma, near Port Alfred into two main groups or seaweed communities. The western-most sites are again divided into two from Plettenberg Bay westwards and another from there eastwards to Kleinemonde. The eastern group is further split into two groups in the region of Qora River near the Kei River and Morgans Bay.

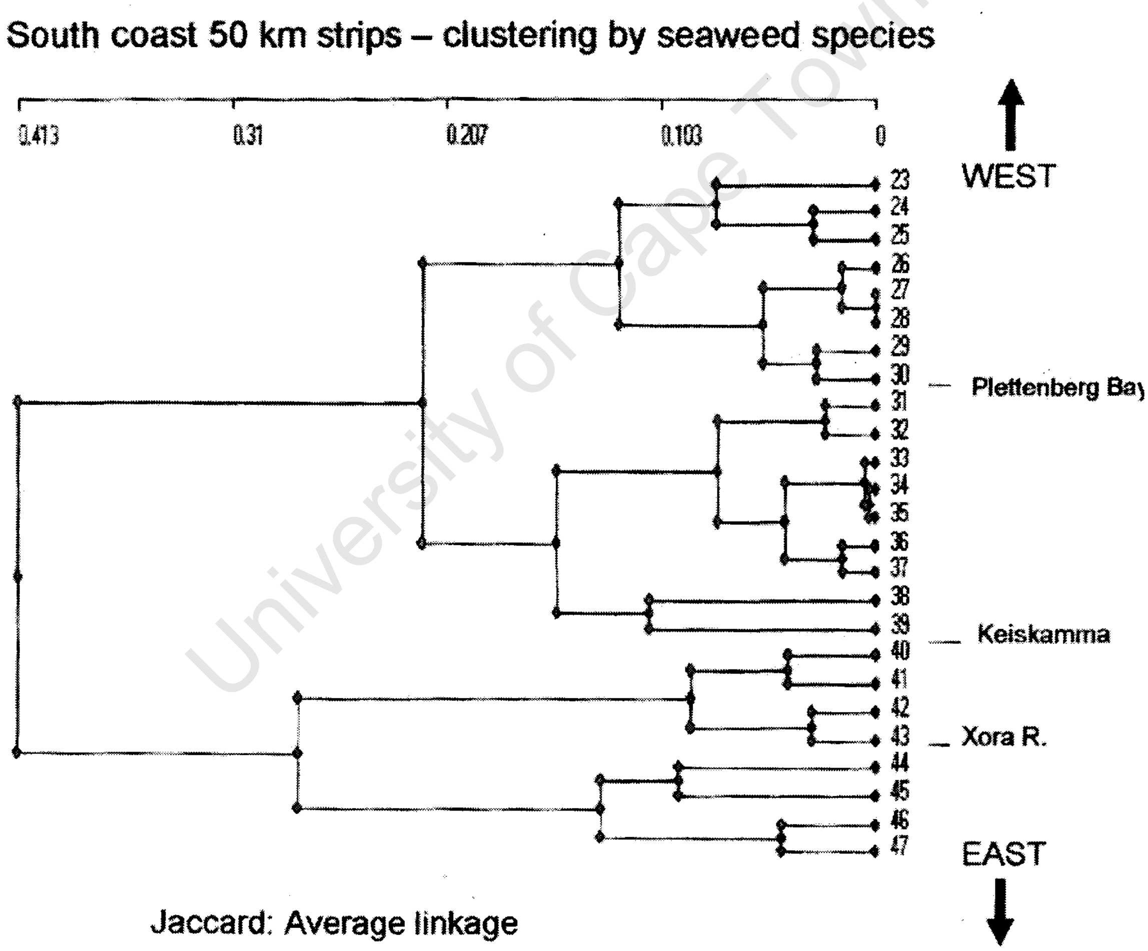

Figure 3.27: Cluster analysis based on updated lists of Bolton, Anderson and Stegenga (unpublished) with the numbers representing the different sections along the coastline. These coastal sections (23-47) cover the coastal range of the present investigation.

Chapter 4: Discussion

Ecology

The biomass and number of species of algae structures a community and with the variation of these in different areas around the coast, different communities are developed. Along the south coast of South Africa the algal species composition of these shallow subtidal communities varies quite considerably. In general as one moves west to east from Still Bay to Mzamba, there was an increase in algal biomass (excluding Silaka and Mzamba) but the number of species generally remained unchanged. The western-most sample sites in this study had the lowest biomass whilst Glen Muir and Beach Rock were found to be the two sites with the highest average biomass. Previous studies (Stegenga & Bolton 1992, Bolton & Stegenga 2002) have suggested that the south coast of South Africa has higher species diversity relative to the west coast. Other studies (Bolton 1994, Bolton & Anderson 1997, Bolton *et al.* 2004) looking at the global diversity patterns, have said that the species diversity along coastlines, whether it is a temperate or a tropical area, remains relatively similar. However, these studies are on a biogeographic scale (units of 50km of coastline or more) and are based on global seaweed patterns or use information from previous seaweed collections and species lists.

Some areas, both globally and locally are better studied than other areas, i.e. in South Africa the Cape Peninsula region and generally the intertidal zone is better studied (Brown & Jarman 1978, Farrell *et al.* 1994, Bolton & Anderson 1997, Bolton & Stegenga 2002). This may lead to higher number of species in this area than in areas of less study, therefore giving a false impression of seaweed diversity. This study found not only a moderately low species diversity (less than 100 species) but also a relatively constant species diversity in community composition in this marine province. One must remember however that this study was undertaken in a habitat that has been sampled very little (i.e. the shallow subtidal zone) and over a very small area, with a total of only 85 quadrats sampled for the whole of the south coast area. Evans (2005) undertook a similar study in the subtidal zone of the KwaZulu-Natal coast. The study reported a high diversity of species (294 taxa) in just 71 quadrats that totalled an area of 4.44m^2 (as compared with the present study reporting 97 species in an area 21.25m^2). Despite this high number of species, Evans (2005) found a relatively low total biomass (2420.8g) and this was because the seaweeds dominating this area were turf-forming algae, that is generally small growing filamentous algae. Thus seaweed communities have a great diversity per m^2 on the east compared with the south coast, although the flora available on a 50km stretch of coastline is similar in the two regions.

The higher biomass found at Glen Muir, Haga Haga and Beach Rock may be attributed to the lower temperature range found in this area (roughly 2.8°C), which allows for the growth of a wider range of algae. Sea conditions in the Agulhas Marine Province (especially in the Agulhas Bank region) are very variable with a wide range of sea temperatures in this area (Zoutendyk 1973, Brown & Jarman 1978). Previous studies (Breeman 1988, Lüning 1990, Bolton & Anderson 1990, 1997) have proven that seaweed distribution and community composition are correlated with seaweed temperature regime. The current study also finds a correlation between the temperature regime and seaweed communities (Figure 3.15). A stable or relatively stable sea surface temperature could possible provide a more consistent environment for perennial algal species to grow to a large size. For example, Glen Muir, Beach Rock and Haga Haga have temperature ranges amongst the lowest (2.8 °C, 2.9 °C and 3.4°C respectively), and also have amongst the highest biomasses across the eleven study sites.

The increasing biomass moving from west to east and peaking in the Glen Muir region may also be attributed to the increase in number of Chlorophyta species at this site (as well as high incidence of articulated coralline algae) (Figure 3.3). Many of the green algal species found in this study were large growing species with a high biomass (42% of the biomass) (Table 3.1) relative to that of both red and brown species. This biomass pattern could also possibly be attributed to changes in nutrient levels and the degree of impact from large grazers (especially fish) that varies from site to site (although these variables were not measured).

The number of Chlorophyta and Phaeophyta species was generally low compared with red algal species. Although the green algae only contribute 12.4% to the number of species, they did contribute 42.8% to the total biomass, and this can be attributed to the high biomass of *Caulerpa filiformis* (Table 3.4). Table 3.4 also shows that there was a high biomass of coralline algae, with over 20% of the total biomass being *Amphiroa ephedraea.*

Brown algae on the other hand contributed little to both the number of species and the biomass (just 14.4 % and 2.1% respectively). Bolton (1996) suggested that brown algal diversity on a global scale is limited by upwelling, which does not occurs very often along the south coast but is more common on the west coast. Bolton (1996) also says that South Africa has fewer temperate brown algae than other temperate regions. This could possibly be why very few species of brown algae, and a low biomass of this group, was found across all of the study sites.

The group of algae classified in this study as other red algae (i.e. Rhodophyta that are not corallines) contribute 55.7% to the total number of species but only 10.4% to the total biomass, however they are the most abundant (or commonly found group of algae) at nine of the eleven sample sites (Figure 3.4). The species that were found tend to have small growth forms (e.g. *Acrosorium maculatum, Ceramium camouii and Nienburgia serrata)* and contribute little to the total biomass.

The coralline algae contributed only 17.5% to the total number of species but, as with the Chlorophyta, contributed greatly to the biomass (44.7%). Corallines along this coast were found to be abundant at all of the sites, with the highest biomass at nine of the eleven sites (Figure 3.2). They featured predominately in terms of biomass and frequency of occurrence (Table 3.3 and 3.4), with certain species occurring in over 30 of the quadrats, and *Amphiroa ephedraea* having the second highest biomass. Previous studies have highlighted the importance coralline algae play, not only on the south coast of South Africa, but also in many other rocky shore communities (Johansen 1981, Anderson & Stegenga 1989, Lüning 1990). They are relatively resistant to grazing, can grow to large sizes (up to 30cm) and are generally superior competitive species (Johansen 1981, Bold & Wynne 1985, Anderson & Stegenga 1989). This competitive advantage may be attributed to their diversity of adaptations, as well as their ability to grow in various marine habitats with both warm and cold water and also in areas where there are low light intensities (Johansen 1981, Bold & Wynne 1985). Many coralline algal species (i.e. several species of *Amphiroa*) are adapted to living on crowded shores by growing on other plant and animal species for part or all of their lifecycle (Johansen 1981, Bold & Wynne 1985) although this is more common in the intertidal zone. Coralline algae are also resistant to grazing as they have hard, calcified cell walls (incorporating calcium carbonate) that make them unpalatable and indigestible for many animals.

Many species of algae were found to occur at several of the sites, i.e. *Arthrocardia carinata* had the highest frequency of occurrence yet it was not even in half the quadrats sampled (it occurred in just 45.5% of the quadrats) (Table 3.3). The species that occurred at most of the eleven sample sites were predominantly coralline algae. *Arthrocardia corymbosa* and *Cheilosporum cultratum* subsp. *multifidum* occurred at ten of the eleven sites and *Amphiroa ephedraea, Arthrocardia carinata* and *Haliptilon subulatum* occurred at nine of the eleven sites. The non-coralline alga that occurred at most sites was *Plocamium suhrii*, being found at eight of the sample sites. Many of these genera that include species in Table 3.3. and 3.4 are known to be well defended against grazing i.e. *Halimeda, Caulerpa, Sargassum, Dictyota* and the articulated corallines (Littler & Littler 1980, Branch & Branch 1981, Steneck & Watling 1982, Bold & Wynne 1985, Littler *et al.* 1986, Paul & Hay 1986, Johansen 1981, Lüning 1990, Bolton & Anderson 1997).

The distribution of seaweed and the structure of algal communities is influenced by numerous factors (Brown & Jarman 1978, Wood 1987, Bolton & Anderson 1990, Santos 1993). Some of these environmental factors were tested within this study, although several did not prove to have a significant influence on the algae communities in the area.

The slope of an area or the substratum topography has not often been studied as a factor influencing community structure. Santos (1993) found that there was a positive relationship between the biomass of *Gelidium sesquipedale* and the substrate slope. In the current study however, the biomass and the number of species remained fairly constant as the slope changed (Figures 3.8 and 3.9). Santos (1993) suggested that turbulent patterns of water flow are enhanced by the presence of obstacles, which are more common on horizontal surfaces. This water movement affects the seaweed development both positively (by increasing nutrients and spore dispersal) and negatively (through mechanical stress on the plants leading to increased mortality or breakage) (Koehl 1986, Lobban *et al.* 1985, Lüning 1990, Santos 1993). The sites in this study were purposefully chosen because they are moderately exposed to waves and strong water movement and at certain times of the year much of the shallow subtidal zone along this entire coast is subject to strong wave action. Therefore the water movement or turbulence caused by the degree of slope may have had a limited influence on the algal community at these study sites. Evans (2005) found that along the KwaZulu-Natal coast, as the depth increased the biomass and species number decreased and attributed this to not only decreased light penetration but also reduced water movement caused by wave action. The current study found similar decreases in biomass with depth, however in this case, it may not be due to decreased light penetration as the depths sampled were relatively shallow.

Grazers are often found to be important factors in the structuring of algal communities (Lawrence 1975, Branch & Branch 1981, Anderson & Stegenga 1989, Bolton & Anderson 1990, Bustamante *et al.* 1995, Bolton & Anderson 1997) however little work has been done on the impact they have on south coast communities. In this study benthic grazers collected in quadrats were found not to significantly influence either the biomass or the number of species (Figure 3.10 and 3.11). It is often difficult, without gut analysis of the animals, to determine their diet and as such, one is unsure of what proportion of macroalgae each different species of grazers consume. The grazers were also not identified to species level thus making it impractical to fully determine from previous work the diets of each of these grazers. In one study (Maneveldt *et al.* 2006) large grazers such as chitons and limpets on the western overlap region (False Bay) of South Africa in the intertidal zone, were found to graze mainly on encrusting corallines. As these encrusting corallines were not considered within this study, and the potential impact of grazing by fish was also not looked at, the full impact of grazers cannot be known.

The depth when compared to the number of species was found not to have a significant impact (Figure 3.7). However when compared with biomass, it was found there was a significantly negative relationship between the two variables (Figure 3.6). As depth increased the biomass decreased as proposed. Depth has been shown in many previous studies to influence the structure of communities with regard to its effects on the amount of light available for photosynthesis (Simons 1976, Lobban *et al.* 1985, Wood 1987, Lüning 1990, Santos 1993, Bolton & Anderson 1997, Lubke 1998, Leliaert *et al.* 2000). As depth increases the light that penetrates the water decreases, thus limiting the amount of photosynthesis and therefore growth that can occur in algal species. Many algae are adapted to low light levels and even thrive in such environments where competition for space with other algal species is low. However the depths that these studies report are relatively deep (i.e. down to depths of 30m) and this study was based in the shallow subtidal zone. As such the depths sampled were shallow (0 - 2.5m) and light attenuation was unlikely to greatly influence the algae, however biomass was still found to decrease with depth.

In order to establish possible reasons for this pattern between depth and biomass, the depth was correlated to the number of grazers (Figure 3.12). As the depth increased, the number of grazers increased significantly and as previously mentioned with increasing depth, there was a decrease in biomass. This decrease in the biomass of seaweed could therefore be attributed to an increase in the number or grazers present, as grazers are known to have an impact on algal communities. It is also possible that the increase in grazers with depth and the biomass decrease with depth are not truly related or correlated to one another. This maybe due to the fact that only certain grazers were included in this study and many other important ones were not counted (i.e. fish). Several species of fish have been found to be important in affecting community structure and biomass of an area (Schupp & Paul 1994), and thus should be included in any future research of these rocky shore environments.

The sea temperature has been found to be one of the most important factors influencing the algal composition of an inshore marine community (Wood 1987, Bolton & Anderson 1990, Lüning 1990, Lobban & Harrison 1994, Bolton & Anderson 1997, Lubke 1998, Lutjeharms 1998, Leliaert *et al.* 2000, Bolton & Stegenga 2002). In the study region the temperature regime is generally seasonal, with occasional cooler upwelling events in some areas. In the current study mean annual temperature was found not to impact either biomass or species diversity (Figure 3.13 and 3.14). However when the biomass was compared with the temperature range of the sites, there was found to be a significant negative relationship ($p = 0.0003$) (Figure 3.15). A large temperature range (or high variation in the sea temperature throughout the year) will create a non-constant or erratic environment in which the seaweed must be adapted to live. With varying conditions in the surrounding water, the seaweed must be able to tolerate bursts of warm and cold water, especially those species found in areas with a high range i.e. Still Bay (7.4°C) and Mossel Bay (6.9 °C). Several species were found at these two sites and not at any of the other study sites. These species include *Callithamnion cordatum, Ceramium* sp.2 and *Colpomenia sinuosa* at both Still Bay and Mossel Bay; and *Ceramium camouii, Falenbergia rufolanosa* and *Gelidium reptans* at Mossel Bay.

It was thought that the mean annual temperature and temperature range may be autocorrelated or interlinked but Figure 3.17 shows that there are different regions on the coast, with different temperature average/range combinations. It can therefore be concluded that mean annual temperature has no significant impact on seaweed communities, but rather when measuring temperature for future research, the temperature range is most important.

The correlation analysis between the biomass and the number of species (Figure 3.17) did not produce a significant relationship. It was hypothesised that the number of species would decrease with an increase in biomass, however this was not found, in fact the number of species remained relatively unchanged as the biomass increased. As previously mentioned, it has been shown that there is a relatively similar number of species around the south coast (Bolton 1994, Bolton & Anderson 1997, Bolton *et al.* 2004) but the biomass varies considerably between sample sites and even the quadrats at each of these sites. The results suggest that there is no overcrowding occurring from large individual species along this shoreline. Although there are a few large species that may dominate certain areas (i.e. *Caulerpa filiformis*), in general other species present are able to compete successfully for both light and space.

Biogeography

Much work has been done to classify coastal areas around South Africa into different biogeographical zones, but most of this has been based mainly on studies of the intertidal zone (i.e. Stephenson 1947, Bolton & Anderson 1997, Bolton 1999). Virtually no work has been done to classify shallow subtidal algal communities into biogeographical distinct regions.

In order to fully distinguish different biogeographical zones, one needs to look at both species diversity and endemism of species (Bolton *et al.* 2004). A length of coastline can be described as a biogeographical region if it has a homogenous biota and is separated by floral (or faunal) discontinuity from the adjacent area (Bolton *et al.* 2004). The level of endemism of the region is often deemed important but is seldom used in this sort of analysis (Bolton *et al.* 2004). This study did not examine the endemism of the algal species, which may limit the ability to distinguish biogeographical breaks along the coast. However, several clear biogeographical patterns emerge from the data.

This study distinguishes somewhat different communities at the most easterly sites. Beach Rock and Silaka are grouped together and separate from the other westerly sites; and Mzamba is separated from all the other sites (Figure 3.19 and 3.21). Mzamba is characterised by species such as *Dictyomenia stephensonii, Inkyuleea beckeri, Martensia elegans* and *Metamastophora flabellata*; whereas Beach Rock and Silaka are characterised by numerous species including *Botryocladia madagascariensis, Cheilosporum proliferum, Dictyota dichotoma var. intricata* and *Heterosiphonia dubia*. These species are east coast species (occurring primarily in the KwaZulu-Natal region) therefore partly explaining the separation of these three sites from the more westerly ones. Figure 3.25 and 3.26 also show a clear break between the Beach Rock and Silaka sites with the other more westerly sites.

The DECORANA plot for the presence/absence data (Figure 3.19) separates the eastern sites (i.e. Mzamba, Silaka and Beach Rock) from the more westerly sites along a biogeographical gradient (axis one). This suggests a strong biogeographical distinction from the other westerly sites. Mzamba is also separated from Beach Rock along axis two which could possibly be a temperature range gradient. Mzamba experiences a large temperature range (4.7°C) compared to Silaka (3.1°C) and Beach Rock (3.0°C), perhaps accounting for different community structures. The DECORANA plot for the biomass (Figure 3.21) suggests that Glen Muir and Haga Haga are separated along a temperature range gradient (axis one) from the other sample sites. These two sites experienced the lowest temperature range and Still Bay (which is on the extreme right of this plot) experiences the highest range in temperatures. This separation of Haga Haga and Glen Muir could be attributed to the high biomass found at these two sites, especially of Chlorophyta, including *Halimeda cuneata* and *Caulerpa* species.

The composition of an algal community is, as previously mentioned, determined by a number of factors, and the differences in these algal communities leads to the formation of biogeographical zones. Figures 3.23 and 3.24 illustrate the factors influencing these breaks between the study sites using presence/absence data and biomass data respectively. The temperature variables found to have the greatest affect were the minimum and maximum monthly temperature and the temperature range (mean annual temperature did not have any significant impact). Figure 3.24 shows that the most westerly sites (i.e. Still Bay and Mossel Bay) were influenced by temperature range and it is these two sites that have the highest temperature range (7.4°C and 6.9°C respectively). It also shows that the most easterly sites (i.e. Mzamba, Silaka and Beach Rock) are influenced greatly by the maximum temperature. These sites have the highest maximum monthly temperatures, namely Mzamba 23.7°C, Silaka 22.2°C and Beach Rock 22.1°C. These sites are the closest in terms of distance to the subtropical east coast province as set out by Stephenson (1948), where tropical and subtropical seaweed species flourish.

The CANOCO for the biomass data (Figure 3.24) shows very similar results to those found when using the presence/absence data (Figure 3.23). However the eigenvalues for the biomass data were much higher than those found for the presence/absence data. From these two CCA plots (and the correlation analysis graphs) it can be said that the most important environmental factors correlated to species composition of shallow subtidal communities in the Agulhas Marine Province are temperature range (greatly affects Still Bay and Mossel Bay), minimum monthly temperature (Beach Rock, Silaka and Mzamba) and maximum (Silaka and Mzamba) monthly temperature (which is undoubtedly linked with temperature range) and depth. However there may be other factors, not sampled in this study, that are important in this zone (e.g. nutrient concentrations as well as biomass and species composition of grazing fish).

The hierarchical clustering using presence/absence data (Figure 3.25) and biomass (Figure 3.26) provide fairly different results. With the presence/absence data the first division separates Beach Rock, Silaka and Mzamba from the other sites pointing to a distinct region incorporating these three sites and representing the warm-water element of the east coast of South Africa. The next division separates Still Bay from the central sites, and the following division separates Port Elizabeth and more westerly sites (excluding Still Bay) from Port Alfred and the more easterly sites (up until Glen Muir). The sixth quadrat at Port Alfred is an outlier and this may be attributed to the quadrat comprising only *Caulerpa filiformis*. Figure 3.26 (the biomass cluster analysis) shows many different groupings or separations with many of the primary divisions separating outlying samples from other samples. The major grouping separates the samples into three groups i.e. Beach Rock and Silaka; Mzamba; and most of the western samples (Still Bay, Mossel Bay, Tsitsikamma, Port Elizabeth and Cape St. Francis). This high number of divisions maybe due to a high variability of the biomass between different sample sites. The lowest biomass recorded was in the third quadrat at Mossel Bay (48.73g) whereas the highest was in the fifth quadrat at

Glen Muir (1997.95g). Even the biomass between the ten Glen Muir samples varied considerably, ranging from 229.94g to 1997.95g.

Stephenson (1948) suggested that there was a break at Port Elizabeth where the warm temperate south coast province ends and the eastern overlap begins. This eastern overlap continues from Port Elizabeth to Port Edward (just east of Mzamba). Bolton & Anderson (1997) suggest that the Agulhas Marine Province runs from Cape Agulhas to East London, from where the eastern overlap begins. The analysis of unpublished data of Bolton, Anderson and Stegenga studying the coastline in 50km sections, found that there were several changes in algal biogeographical structure. A break was found in the vicinity of Port Alfred with the area to the immediate west of this forming a separate biogeographical zone, and the areas to the east forming another zone. The results from Bolton, Anderson and Stegenga (unpubl.) tend to overlap with those found in this current study and therefore help to validate the results. The current study suggests that there is a distinct community or region that extends between Port Alfred and Glen Muir, with the area to the west being a distinct region (i.e. Port Elizabeth eastwards and stopping or experiencing another change at Still Bay). The area to the east is another distinct region (i.e. Beach Rock eastwards), almost certainly with close affinities to the coast of southern KwaZulu-Natal, which it adjoins.

Conclusions

The composition of shallow water (0 – 2.5m) subtidal seaweed communities changes along the South African south coast, between Still Bay and Mzamba (northern Transkei). Both biomass and species composition differ considerably between the eleven sites sampled in this study, although the number of species present remains somewhat constant. Deeper sampling of the area may have revealed more pronounced variations and thus would be beneficial in future studies. However, this study focused primarily on the shallow subtidal, an area where there has been very little previous research, and where there is limited information available regarding the seaweed communities.

Articulated coralline algae were found to be important components of the shallow subtidal zone, with other red species also being abundant. *Arthrocardia* species were particularly common, with *Amphiroa* species providing a lot of the biomass. *Caulerpa filiformis* was not only present at many of the sites, but was also found in extremely large quantities.

The patterns of species distribution and abundance are often determined by a complex interaction of both biotic and abiotic factors (Santos 1993). However in this study it was found that of the factors analysed, only depth and the temperature range had a significant impact on the biomass. Although other environmental factors were considered (i.e. slope, large invertebrate grazers, mean annual sea temperature) these did not appear to have a significant effect on either biomass or number of seaweed species. The minimum and maximum temperatures also affected the seaweed community structure at many of the sites (as shown in Figures 3.23 and 3.24). Seaweed biomass declined with depth (0 - 2.5m) but depth may have been a surrogate for either wave action (which was not measured, but would correlate negatively with depth) or number of grazers (which correlated positively with depth).

Although the hypothesis are primarily ecological, one of the main focuses of the project is to draw conclusions about the biogeography of the area. In order to do this, you need to investigate ecological relationships of an area to fully understand how communities are affected. From there you can identify significant changes in seaweed communities and outline important biogeographical areas. With regard to the hypothesis, the findings are as follows:

- Biomass and number of species did not correlate – rejects H2
- Mean annual sea surface temperature did not correlate with biomass or species number – rejects H1
- Sea surface temperature range does not correlated with species number – rejects H1
- Sea surface temperature range increases with a decrease in biomass – confirms H1

From the results it can also be seen that biomass and species number are not affected by either the slope or the grazer number.

It is thought that wave exposure and sand inundation are often the most important factors (along with temperature) in shaping algal communities (Brown & Jarman 1978, Bolton &

Anderson 1990, Lüning 1990, Lobban & Harrison 1994, Bustamante & Branch 1996, Bustamante *et al.* 1997, Leliaert *et al.* 2000). Although the study sites were chosen to try and preclude the impact of these differing variables (i.e. all study sites were moderately wave exposed and many were not close to areas of sand), it would have been useful to actually measure these factors at all eleven sites to be used in the correlation analysis. Due to weather and time constraints at some of the sample sites, it was, unfortunately, not possible to measure all of these environmental variables. Further work in the subtidal zone (both in shallow and deep water) should therefore include information on wave exposure, sand inundation plus in-depth information on grazers, temperature regime, nutrient levels and competition (both inter- and intraspecific). This would clarify the findings of this current study and improve the understanding of this important marine environment.

There are other factors that need to be considered for future research. The temperature of the water can vary with proximity to the shore, level of wave action and the depth of the water being sampled. Thus comprehensive temperature values should be measured. The slope of the sample site should preferably be measure independently from the depth, with replicate samples at the same depth and location but with different slopes. There may also be seasonal variations in the algal composition of a rocky shore, especially in an area with abundant ephemeral species. It maybe necessary to consider this before undertaking field work in future.

This study encompasses a large area of the South African coast that has not previously received much attention. It highlights which environmental factors are most significant in impacting on shallow subtidal algal communities in this area, and at which point or place, these communities experience a change in composition. Although further work is needed in this zone along the south coast, this current study goes some way into setting in motion any future work and providing a basis for future studies.

References

Anderson, R.J. and H. Stegenga. 1989. Subtidal algal communities at Bird Island, Eastern Cape, South Africa. *Botanica Marina* **32**: 299-311.

Anderson, R.J., Bolton, J.J., Molloy, F.J. and K.W.G. Rothman. 2003. Commercial seaweeds in southern Africa. In *Proceedings of the Seventeenth International Seaweed Symposium.* Eds. Chapman, A.R.O., Anderson, R.J., Vreeland, V.J., and I.R. Davison. Oxford University Press, Oxford. p. 1-12.

Anderson, R.A., McKune, C., Bolton, J.J., De Clerck, O., and E. Tronchin. Patterns in subtidal seaweed communities on coral-dominated reefs at Sodwana Bay on the KwaZulu-Natal coast, South Africa. 2005. *African Journal of Marine Science* **27(3)**: 529-537.

Begon, M. Harper, J.L. and C.R. Townsend. 1996. *Ecology: individuals, populations and communities*. Blackwell Science, Oxford. 1068p.

Boaden, R.J.S. and R. Seed. 1985. *An introduction to coastal ecology*. Blackie and Son Limited, Glascow. 218p.

Bold, H.C. & M.J. Wynne. 1985. *Introduction to the Algae: structure and reproduction.* Second edition. Prentice Hall, New Jersey. 720p.

Bolton, J.J. 1986. Marine phytogeography of the Benguela upwelling system on the west coast of southern Africa: a temperature dependent approach. *Botanica Marina* **29**: 251-256.

Bolton, J.J. 1994. Global seaweed diversity. *Botanica Marina* **37**: 241-245.

Bolton, J.J. 1996. Patterns of species diversity and endemism in comparable temperate brown algal floras. *Hydrobiologica* **326/327:** 173-178.

Bolton, J.J. 1999 Seaweed systematics and diversity in South Africa: an historical account. *Transactions of the Royal Society of South Africa* **54(1)**: 167-177.

Bolton, J.J. and R.J. Anderson. 1990. Correlation between intertidal seaweed community composition and sea water temperature patterns on a geographical scale. *Boanica Marina* **33:**447-457.

Bolton, J.J. and R.J. Anderson. 1997. Marine vegetation. In *Vegetation of southern Africa.* eds Cowling, R.M., Richardson, D.M. and S.M Pierce. Cambridge University Press, Cambridge. p. 348- 375.

Bolton, J.J., Coppejans, E., Anderson, R.J., De Clerk, O., Samyn, Y., Leliaert, F. and A.S. Thander. 2001. Biodiversity of seaweeds and echinoderms in the western Indian Ocean. *South African Journal of Science* **97**:453-545.

Bolton, J.J., Leliaert, F., De Clerck, E., Anderson, R.J., Stegenga, H., Engledow, E. and E. Coppejans. 2004. Where is the western limit of the tropical Indian Ocean seaweed flora? An analysis of intertidal seaweed biogeography on the east coast of South Africa. *Marine Biology* **144**: 51-59.

Bolton, J.J. and H. Stegenga. 1987. The marine algae of Hluleka (Transkei) and the warm temperate/sub- tropical transition on the east coast of southern Africa. *Helgoländer Meeresunters*. **41**:165-183.

Bolton, J.J. and H. Stegenga. 1990. The seaweeds of De Hoop Nature Reserve and their phytogeographical significance. *South African Journal of Botany* **56(2)**: 233-238.

Bolton, J.J. and H. Stegenga. 2002. Seaweed species diversity in South Africa. *South African Journal of Marine Science* **24**: 9-18.

Branch, M. and G. Branch. 1981. *Living shores of Southern Africa*. Struik Publishers, Cape Town. 272p.

Breeman, A.M. 1988. Relative importance of temperature and other factors in determing geographic boundaries of seaweeds: experimental and phonological evidence. *Helgoländer Meeresunters.* **42**: 199-241.

Brown, A.C. and N. Jarman. 1978. Coastal marine habitats. In *Biogeography and ecology of Southern Africa 2.* ed Werger, M.JA. Junk, The Hague. p 1239-1277.

Bustamante, R.H., Branch, G.M., Eeskhout, S., Robertson, B., Zoutendyk, P., Schleyer, M., Dye, A., Hanekom, N., Keats, D., Jurd. M., and C. McQuaid. 1995. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia* **102**: 189-201.

Bustamante, R.H., and G.M. Branch. 1996. Large scale trophic structure of southern African rocky shores: the roles of geographic variation and wave exposure. *Journal of Biogeography* **23**: 339-351.

Bustamante, R.H., Branch, G.M., and S. Eekhout. 1997. The influences of physical factors on the distribution and zonation patterns of South African rocky-shore communities. *South African Journal of Marine Science* **18**: 119-136.

Chatfield, C. and A.J. Collins.1980. *Introduction to multivariate analysis.* Chapman and Hall, London. 246p.

Critchley, A.T., Gillespie, R.D. and K.W.G. Rotmann. 1998. The seaweed resources of South Africa. In *Seaweed resources of the world.* eds. Critchley, A.T. and M. Ohno. Japan International Cooperation Agency. p 413- 416.

De Clerk, O., Bolton, J.J., Anderson, R.J. and E. Coppejans. 2005. Guide to the seaweeds of KwaZulu-Natal. *Scripta Botanica Belgica* **33:**13-37.

De Riddler, C. and M. Lawrence. 1982. Food and feeding mechanisms: Echinoidea. In *Echinoderm nutrition*. eds. Jangoux, M. and J.M. Lawrence. A.A. Balkema, Rotterdam. p 57-58.

Emanuel, B.P., Bustemante, R.H., Branch, G.M., Eekhout, S. and F.J. Odendaal. 1992. A zoogeographical and functional approach to the selection of marine reserves on the west coast of South Africa. *South African Journal of Marine Science* **12:**341-354.

Evans, A. 2005. An investigation into the ecology and biogeography of subtidal seaweed communities of KwaZulu-Natal. Masters thesis, University of Cape Town. 97p.

Farrell, E.G., Critchley, A.T. and M.E. Aken. 1993. The intertidal flora of Isipingo Beach, Natal, South Africa, and its phycogeographical affinities. *Helgoländer Meeresunters.* **38**: 227-257.

Farrell, E.G., Critchley, A.T., Aken, M.E. and R.N. Pienaar. 1994. The biogeographical affinities of the seaweed flora of Natal, South Africa, as typified by Isipingo Beach: a multivariate approach. *Botanica Marina* **37**: 272- 285.

Field, J.G. and C.L Griffiths. 1990. Littoral and sublittoral ecosystems of Southern Africa. In *Ecosystems of the world 24: Intertidal and littoral ecosystems.* eds. Mathieson, A.C. and P.H. Nienhuis. Elseveir, New York. p 323-330.

Foster, M.S., Dean, T.A. and L.E. Deysher. 1985. Subtidal Techniques. In *Handbook of phycological methods: Ecological field methods: macroalgae*. eds. Littler, M.M. and D.S. Littler. Cambridge University Press, Cambridge. P. 199-232.

Fricke, A.H. 1979. Kelp grazing by the common sea urchin *Parenchinus angulosus* Leske in False Bay, Cape. *South African Journal of Zoology* **14**: 143-148.

Greenwood, P.J. 1980. Growth, respiration and relative energy budgets for two populations of the sea urchin *Parenchinus angulosus* (Leske). *East Coast Marine Science* **10**: 347-367.

Hay, M., and W. Fenical. 1988. Marine plant- herbivore interactions: the ecology of chemical defence.*Annual Review Of Ecological Systems* **19**: 111-145.

Heydorn, A.E.F., Bang, N.D., Pearce A.F., Flemming B.W., Cater, R.A., Schleyer, M.H., Berry, P.F., Hughes, G.R., Bass, A.J., Wallace, J.H., van der Elst, R.P., Crawford, R.J.M. and P.A Shelton. 1978. Ecology of the Agulhas region: an assessment of biological responses to environmental parameters in the South-west Indian Ocean. *Transactions of the Royal Society of South Africa* **43(2)**: 151-189.

Hoek, C. van den. 1984. Worldwide latitude and longitude seaweed distribution patterns and their possible causes, as illustrated by the distribution of Rhodophytan genera. *Helgoländer Meeresunters*. **38**: 227-257.

Hommersand, M.H. 1986. The biogeography of the South African marine red algae: a model. *Botanica Marina* **29**: 257-270.

Jackelman,J.J., Stegenga, H.S. and J.J. Bolton. 1991. The marine benthic flora of the Cape Hangklip area and its phytogeographical affinities. *South African Journal of Botany* **57**: 295 – 304.

Johansen, H.W. 1976. Phycological reviews 4: Current status of generic concepts in coralline algae (Rhodophyta). *Phycologia* **15**:221.

Johansen, H.W. 1977. The articulated Corallinaceae (Rhodophyta) of South Africa: 1. *Cheilosporum (Decaisne) Zanardini*. *Journal of South African Botany* **43(3):** 163-185.

Johansen, H.W. 1981. *Coralline algae: a first synthesis*. CRC Press, Florida. 239p.

Kent, M. and P. Coker. 1992. *Vegetation description and analysis : a practical approach.* CRC Press, London. 363p.

Knox, G.A. 2000. *The ecology of seashores*. CRC Press, London. 557p.

Knorpinen, S., Jormalainen, V., and T. Honkanen. 2007. Effects of nutrient, herbivory, and depth on the macroalgal community in the rocky sublittoral. *Ecology* **88(4)**: 839-852.

Koehl, M.A.R. 1986. Seaweeds in moving water: form and mechanical function. In *On the economy of plant form and function.* eds. Givnish, T. J. Cambridge University Press, New York. p. 603-634.

Largier, J.L. and V.P. Swart. 1987. East-west variation in thermocline breakdown on the Agulhas Bank *South African Journal of Marine Science* **5(1)**: 263-272.

Lawrence, J.M. 1975. On the relationship between marine plants and sea urchins. *Oceanography Marine Biology Annual Review.* **13**: 213-286.

Leliaert, F., Anderson, R.J., Bolton, J.J. and E. Coppejans. 2000. Subtidal understorey algal community structure in Kelp beds around the Cape Peninsula (Western Cape, South Africa). *Botanica Marina* **43**: 359-366.

Leliaert, F., De Clerck, O., Bolton, J.J. and E. Coppejans. 2001. New records of the Chlorophyta from South Africa, with the emphasis on the marine benthic flora of KwaZulu-Natal. *S. Afr. J. Bot.* **67**: 450-459.

Little, C. and J.A. Kitching. 1996. *The biology of rocky shores.* Oxford University Press, Oxford: 240p.

Littler, M.M. and D.S. Littler. 1980. The Evolution of Thallus Form and Survival Strategies in Benthic Marine Macroalgae: Field and Laboratory Tests of a Functional Form Model. *The American Naturalist* **116(1)**: 25-44.

Littler, M.M., Taylor, P.R. and D.S. Littler. 1986. Plant defence in the marine environment. *Coral Reefs* **5(2)**: 63-71.

Lobban, C.S. and P.J. Harrison. 1994. *Seaweed ecology and physiology.* Cambridge University Press, Cambridge. 366p.

Lobban, C.S., Harrison, P.J. and M.J. Duncan. 1985. *The physiological ecology of seaweeds.* Cambridge University Press, New York. 242p.

Lubke, R.A. 1998. Descriptions of the coastal regions. In *A field guide to the Eastern Cape coast.* eds Lubke, R.A., F.W. Gess and M.N. Bruton. The Grahamstown centre of the Wildlife society of Southern Africa. p 3-9.

Lubke, R.A. and S.C. Seagrief. 1998. Marine algae. In *A field guide to the Eastern Cape coast.* eds Lubke, R.A., F.W. Gess and M.N. Bruton. The Grahamstown centre of the Wildlife society of Southern Africa. p 65-116.

Lüning, K. 1990. *Seaweeds. Their environment, biogeography and ecophysiology.* John Wiley and Sons, Inc, New York. 527p.

Lutjeharms, J.R.E. 1998. Coastal Hydrogeography. In *A field guide to the Eastern Cape coast.* eds Lubke, R.A., F.W. Gess and M.N. Bruton. The Grahamstown centre of the Wildlife society of Southern Africa. p. 50-64.

Maneveldt, G., Wilby, D., Potgieter, M. and M. Hendricks. 2006. The role of encrusting coralline algae in the diets of selected intertidal herbivores. *Journal of Applied Phycology* **18:**619-627.

McQuaid, C.D. and G.M. Branch. 1984. Influence of sea temperature, substratum and wave exposure on rocky intertidal communities: an analysis of faunal and floral biomass. *Marine Ecology Progress Series* **19**: 145-151.

Paul, V.J. and M.E. Hay. 1986. Seaweed susceptibility to herbivory: chemical and morphological correlates. *Marine Ecology progress series* **33**:225-264.

Pisces 2007. Pisces Conservation Ltd. Lymington, UK.

Ross, G.J.B. 1988. Coastal hydrography. In *A field guide to the Eastern and Southern Cape coast.* eds Lubke, R.A., Gess F.W. and M.N. Bruton. The Grahamstown centre of the Wildlife society of Southern Africa.

Santelices, B., Bolton, J.J. and I. Meneses. In press. Marine algal communities. In *Marine Macroecology.* eds Whitman, J.D. and K. Roy. University Press, Chicago.

Santos, R. 1993. A multivariate study of biotic and abiotic relationships in a subtidal algal stand. *Marine Ecology Progress. Series* **94:**181-190.

Schupp, P.J. and V.J. Paul. 1994. Calcium carbonate and secondary metabolites in tropical seaweeds: variable effects on herbivorous fishes. *Ecology* **75(4):**1172-1185.

Seagrief, S.C. 1967. *The seaweeds of the Tsitskamma Coastal Park.* Pretoria: National Parks Board of Trustees. 147p.

Seagrief, S.C. 1988. Marine Algae. In *A field guide to the Eastern Cape coast.* eds Lubke, R.A., F.W. Gess and M.N. Bruton. The Grahamstown Centre of the Wildlife Society of Southern Africa. p 35-72.

Shannon, L.V. 1985. The Benguela ecosystem.I. Evolution of the Benguela. Physical features and processes. *Oceanographic and Marine Biology Annual Review* **23:**105-182.

Simons, R.H. 1976. Seaweeds of Southern Africa: guidelines for their study and identification. *Fisheries Bulletin* **7:**1-113.

South, G.R. and A. Whittick. 1987. *Introduction to phycology.* Blackwell Scientific Publications, Oxford. 341p.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdana, Z.A. Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A., and J. Robertson. 2007. *Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas.* BioScience **57(7):** 573-583.

Stegenga, H. and J.J. Bolton. 1992. Ceramiaceae (Rhodophyta) of the Cape Province, South Africa: distribution in relation to concepts of marine provinces. *Botanica Marina* **35**: 99-107.

Stegenga, H., Bolton, J.J. and R.J. Anderson. 1997. Seaweeds of the South African west coast. University of Cape Town. 655p.

Steneck, R.S. and L. Watling. 1982. Feeding capabilities and limtitaions of herbivorous molluscs: A functional group approach. *Marine Biology* **68(3)**: 507-522.

Stephenson, T.A. 1944. The constitution of the intertidal fauna and flora of South Africa. II. *Annual Natal Museum* **10**: 261-358.

Stephenson, T.A. 1947. The constitution of the intertidal flora and fauna of SA III. *Annual Natal Museum* **11**: 207- 324.

Stephenson, T.A., Stephenson, A. and du Toit, C.A. 1937. The South African intertidal zone and its relation to ocean currents 1. A temperate Indian Ocean shore. *Trans. Roy. Soc. S. Afr.* **24**: 341-482.

Walker, N.D.1989. Sea surface temperature-rainfall relationships and associated ocean-atmosphere coupling mechanism. PhD. thesis. 173p.

Woelkerling, W.J. 1988. *The coralline red algae: an analysis of the genera and subfamilies of nongeniculate Corallinaceae*. Oxford University Press, Oxford. 268p.

Wood, E. 1987. *Subtidal ecology*. Edward Arnold Ltd, London. 125p.

Zoutendyk, P. 1973. The biology of the Agulhas Sole, *Austroglossus pectoralis*, Part 1. Environment and Trawling Grounds. *Transactions of the Royal Society of South Africa* **40:** 349-366

Appendix 1: Algae species list

Acrosorium acrospermum (J. Agardh) Kylin

Acrosorium maculatum (Sonder ex Kützing) Papenfuss

Amphiroa anceps (Lamarck) Decaisne

Amphiroa beauvoisii J.V. Lamouroux

Amphiroa bowerbankii Harvey

Amphiroa ephedraea (Lamarck) Decaisne

Anotrichium tenue (C. Agardh) Nägeli

Apoglossum spathulatum (Sonder) Womersley & Shepley

Arthrocardia carinata (Kützing) Johansen

Arthrocardia corymbosa (Lamarck) Decaisne

Arthrocardia flabellata (Kützing) Manza

Botryocladia madagascariensis G. Feldmann

Calliblepharis fimbriata (Greville) Kützing

Callithamnion cordatum Børgesen

Carpoblepharis sp.

Carpomitra longicarpa Simons

Caulerpa bartoniae G. Murray

Caulerpa filiformis (Suhr) K. Hering

Caulerpa holmesiana G. Murray

Caulerpa zeyheri Kützing

Ceramiae indet

Ceramium camouii E.Y. Dawson

Ceramium sp. 1

Ceramium sp. 2

Chaetomorpha spiralis Okamura

Champia compressa Harvey

Cheilosporum cultratum subsp. *multifidum* (Kützing) Johansen

Cheilosporum proliferum (J.V. Lamouroux) Hariot

Cheilosporum sagittatum (J.V. Lamouroux) Areschoug

Codium lucasii Setchell

Codium lucasii subsp. *capense* P.C. Silva

Codium stephensiae Dickinson

Colpomenia sinuosa (Mertens ex Roth) Derbès & Solier

Corallina officinalis Linnaeus

Corallina sp. 1

Corallina sp.2

Dasya scoparia Harvey

Delesseria sp.

Derbesia sp.

Dichotomaria diesingiana (Zanardini) Huisman, J.T. Harper & G.W. Saunders

Dictyomenia stephensonii Papenfuss

Dictyopteris ligulata (Suhr) O.C. Schmidt

Dictyota dichotoma (Hudson) J.V. Lamouroux

Dictyota dichotoma var. *intricata* (C. Agardh) Greville

Dictyota liturata J. Agardh

Erythroglossum sp.

Exallosorus harveyanus (Pappe ex Kützing) J.A. Phillips

Falkenbergia rufolanosa (Harvey) F. Schmitz

Gelidium abbottiorum R.E. Norris

Gelidium pteridifolium R.E. Norris, Hommersand & Fredericq

Gelidium reptans (Suhr) Kylin

Gracilaria beckeri (J. Agardh) Papenfuss

Griffithsia confervoides Suhr

Halimeda cuneata K. Hering

Haliptilon subulatum (J. Ellis & Solander) Johansen

Heterosiphonia dubia (Suhr) Falkenberg

Hypnea rosea Papenfuss

Hypnea tenuis Kylin

Inkyuleea beckeri (F. Schmitz ex Mazza) H.-G.Choi, Kraft & Saunders

Jania adhaerens J.V. Lamouroux

Jania crassa J.V. Lamouroux

Jania intermedia (Kützing) P.C. Silva

Laurencia complanata (Suhr) Kützing

Laurencia flexuosa Kützing

Laurencia glomerata (Kützing) Kützing

Laurencia natalensis Kylin

Laurencia obtusa (Hudson) J.V. Lamouroux

Martensia elegans K. Hering

Metamastophora flabellata (Sonder) Setchell

Nienburgia serrata (Suhr) Papenfuss

Peyssonnelia capensis Montagne

Peyssonnelia replicata Kützing

Platysiphonia miniata (C. Agardh) Børgesen

Plocamium beckeri F. Schmitz ex Simons

Plocamium corallorhiza (Turner) J.D. Hooker & Harvey

Plocamium rigidum Bory de Saint-Vincent

Plocamium suhrii Kützing

Polysiphonia incompta Harvey

Portieria hornemannii (Lyngbye) P.C. Silva

Portieria tripinnata (Hering) De Clerck

Pseudocodium de-vriesii Weber-van Bosse

Pterosiphonia cloiophylla (C. Agardh) Falkenberg

Pterosiphonia stangeri (J. Agardh) Falkenberg

Rhodymeniaceae sp.

Rhodymenia natalensis Kylin

Rhodymenia sp.

Sarcodia dentata (Suhr) R.E. Norris

Sargassum heterophyllum C. Agardh

Sphacelaria brachygona Montagne

Spyridia cupressina Kützing

Spyridia horridula F. Schmitz ex J. Agardh

Stypocaulon funiculare (Montagne) Kützing

Stypopodium multipartitum (Suhr) P.C. Silva

Stypopodium zonale (J.V. Lamouroux) Papenfuss

Valonia macrophysa Kützing

Zonaria harveyana (Pappe ex Kützing) Areschoug

Zonaria subarticulata (J.V. Lamouroux) Papenfuss